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STUDIES ON THE MECHANISM OF PARTHENOGENESIS

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I. SPECIAL PART.

1. THE NOMENCLATURE OF THE APOMICTIC PHENOMENA.

IN his work published in 1908 WINKLER defined apomixis as »den Ersatz der geschlechtlichen Fortpflanzung durch einen anderen, ungeschlechtlichen nicht mit Kern- und Zellverschmelzung verbundenen Vermehrungsprozess». In 1878 DE BARY coined the term apogamy for the same thing. As this term has in the course of years been employed to denote different things WINKLER's term is certainly to be preferred.

The conception of automixis includes the amphimictic phenomena by means of which cells or nuclei originating from the same mother-cell fuse after having developed. In the lower animals they occur very frequently. The term has since been applied quite correctly to other groups of animals (see ANKEL, 1927, 1929), where however it has come to denote a sub-division of parthenogenesis. According to WINKLER's definition of apomixis (including parthenogenesis) this grouping is impossible. Being a process of fertilization (even if the nuclei have the same origin) automixis should unquestionably be grouped under amphimixis. See further p. 63.

The first division of the apomictic phenomena in plants must be in those in which the zygoid generation arises in the fructification organs themselves without fertilization, and those in which the propagative organs develop from cells, which do not originate from the fructification organs. A comprehensive term for the former kind of abnormality is TÄCKHOLM's term »agamospermy» (1922). The latter type of phenomena in plants may, as suggested by ERNST (1918), be divided into apocarpy and apoflory, according as the propagative organs are formed in the flowering region and its equivalent in lower plants or not.

The agamospermous phenomena form two terminological groups. One group consists of those cases where an agamospermous gameto-

phyte is present, and comprises apospory, parthenogenesis and apogamety. The other group comprises those instances in the phanerogams in which the embryo is developed direct from a zygoid nucellus cell, not from any cell in a gametophyte: nucellar embryony.

With regard to the parthenogenetic phenomena named so by me according to WINKLER (1908) and ROSENBERG (1930) three different terminological conceptions have prevailed, viz. WINKLER's, STRASBURGER's (1909) and ERNST's (1918). WINKLER correctly attaches the greatest importance as to whether it is an egg-cell in the gametophyte that develops into an embryo. STRASBURGER employs the chromosome numbers as the basis of his classification, so that for him parthenogenesis is only the development of an azygoid egg-cell and apogamy all kinds of propagation from zygoid cells. To ERNST again the essential point is whether the plant and animal species in question is capable of sexual development or not. To him parthenogenesis is therefore the development of gametes in a sexually differentiated species of plant and animal capable of sexual development, apogamy is the *obligatory* apomictic formation of seed from egg-cells and somatic cells in diploid or polyploid gametophytes in hybrids and progenies of hybrids.

Evidence in favour of WINKLER's view is provided, among other things, by the fact that embryo-sacs with zygoid numbers behave like normal azygoid sacs as regards the number, divisions, location and appearance of the nuclei. Egg apparatus, antipodes, polar nuclei are formed, and very often the polar nuclei also fuse (v. ROSENBERG, 1930, p. 35).

In this work parthenogenesis is thus defined, in accordance with WINKLER and ROSENBERG, as the process by means of which an azygoid (haploid) or a zygoid (diploid) *egg-cell is produced and then develops without any fusion of nuclei and cells.*

WINKLER makes a distinction between generative and somatic parthenogenesis. But as these partial terms may suggest the idea that a purely somatic process is the cause of the origin of the egg-cell having the zygoid number, we shall employ here, as in the case of animals, the terms azygoid and zygoid parthenogenesis (v. for instance PRELL, 1923, and ANKEL, 1929). The expressions haploid and diploid parthenogenesis used by many investigators are not employed either, owing to the dual meaning of the terms haploid and diploid.

For the rarely occurring instances of synergid, antipode or polar nuclear embryos in the phanerogams WINKLER employs the term

apogamy. This word has, however, been misused so much, and being besides more adequate, the term apogamety coined by RENNER is to be preferred. This can be used also for the lower plants.

There remains the phenomenon of apospory. CHIARUGI (1926) has divided apospory into »aposporia goniale» and »aposporia somatica». In the former the gametophyte develops from a spore mother-cell, in the latter it develops from a purely somatic cell. The so-called *Antennaria* scheme, which according to earlier investigations showed a purely somatic division in the E.M.C., should therefore be regarded as an »aposporia goniale». According to my criticism (1934 b, 1935) the *Antennaria* scheme has not a somatic division either: closer investigations have shown that in many cases the division *resembles* a somatic division. The difference lies in the appearance of the resting stage, the prophase and frequently in that of the metaphase. Nevertheless, the *Antennaria* scheme, as understood hitherto, forms an evident transition to aposporia goniale. I employ the following definitions:

Apospory is the formation of a gametophyte by *purely somatic divisions*. Generative apospory (ROSENBERG, 1930) is the development of the gametophyte from an E.M.C. or a cell homologous with it in the nucellus (for instance *Alchemilla*, *Oxyria digyna*). Somatic apospory is the development of the gametophyte from an indubitably somatic cell. Azygoid apospory is present if the aposporial gametophyte has a reduced chromosome number and zygoid apospory if it has the zygoid number.

To denote biotypes which propagate themselves apomictically TURESSON (1926) suggested the term apomicts, and those which multiply partly by sexual reproduction and partly apomictically he called amphiapomicts or apoamphimicts, according to the predominant mode of propagation. These terms will be employed in the following pages. To cover the higher taxonomical units, to which the solitary apomicts group themselves in nature, TURESSON (1929) proposed the name agamospecies, provided the biotypes are entirely apomictic; the corresponding term for facultatively sexual groups should be amphiagamospecies. An examination of the fitness of these terms with special regard to the genera *Taraxacum*, *Rubus*, *Rosa* and *Archieracium* will be made later on.

2. MATERIAL AND METHODS.

The *Taraxacum* material examined was to a great extent derived from seeds obtained from Dr. G. HAGLUND, Lund, Prof. G. SAMUELSSON,

TABLE 1. *Cytologically Examined Material Regarding the Course of Meiosis.*

	Determined by	Locality	Chromosome Number	Meiosis examined in
Taraxacum				
Erythrosperma				
T. fulvum RAUNK.	HAGLUND	Bornholm	32	♂♀
T. ruberulum BORGW. et DT.	BORGWALL	Gothenburg	24	♂♀
T. tenuilobum DT.	HAGLUND	Riga	24	♂♀
T. 1930:267, T. brachyglossum DT.?	BORGWALL	Gothenburg	24	♀
T. 1930:685		Intermixture?	32	♀
T. 1930:1		Malmö	24?	♂
Spectabilia				
T. croceum DT.		Bot. Gn. Kovno	32	♂♀
T. 1930:719		Lapland	32	♂♀
T. 1930:302		»	32	♂♀
T. 1930:409		Bot. Gn. Edinburgh	32	♂
T. 1930:653		Lapland	32	♀
Vulgaria				
T. melanthoides DT.	HAGLUND	Småland	24	♂
T. litorale RAUNK.	»	Latvia	24	♂♀
T. sublaeticolor DT.	DAHLSTEDT	Lidingö	24	♀
T. Ekmani DT.	HAGLUND	Scania	24?	♀
T. retroflexum LINDB. fil.	DAHLSTEDT	Lidingö	24	♀
T. laeticolor DT.	HAGLUND	Småland	24	♂♀
T. 1930:679		Gotland	24	♂♀
T. 1929:5		Leningrad	24	♂♀
T. 1930:181		Gotland	24	♂
T. 1929:8		Roston Don	24	♂
T. »Arjeploug 4»		Lapland	24	♂♀
T. haematopus DT.	»	Bornholm	24	♀
Maculigera				
T. maculigerum LINDB. fil.	»	Småland	24	♂
T. praestans LINDB. fil.	»	Småland and Bornholm	24	♂♀
T. Nordstedtii DT.	»	Småland	48	♂♀
Dissimilia				
T. dissimile DT.	»	Memel	24	♂♀
T. pseudofulvum LINDB. fil.	»	Finland	?	♀
Palustria				
T. palustre EHRH. coll.	HANDEL MAZZETTI	Austria	24	♂
T. lanceolatum POIR.	CH. D. ALLEIZETTE	Landau	32	♂

	Determined by	Locality	Chromosome Number	Meiosis examined in
T. balticum DT.		Gothenburg	32	♂♀
T. ad *scaturiginosum* HAGL.	HAGLUND	Greece	24	♀
Ceratophora				
T. ecorniculatum HAGL. in sched.	»	China	32	♂
T. deliciosum HAGL. in sched.	»	»	24	♂
T. 1930 : 712		Lapland	32	♀
T. 1930 : 671		»	32	♂♀
T. 1930 : 714		»	32	♂♀
T. ceratophorum LEDEB. coll.	HANDEL MAZZETTI	Tyrol	32	♀
Alpina				
T. Kalbfussi HAND. MAZZ. ...	»	»	24	♂♀
T. alpinum (HPPE) KOCH coll.	»	»	32	♂♀
T. alpinum (HPPE) KOCH coll. (× *Pacheri* SCH. et BIP.?)...	»	»	24	♂♀
Euerythrocarpa				
T. amborum HAGL.	HAGLUND	Greece	24	♂♀
T. fontanum HAND. MAZZ. ...	HANDEL MAZZETTI	Tyrol	32	♂♀
T. Samuelssonii DT.	SAMUELSSON	The Alps	32	♂♀
T. porphyranthum BOISS. ...		Bot. Gn. Gothenburg	24	♀
T. 1930 : 672		Jarkend	32	♂♀
T. bessarabicum HAND. MAZZ.		Hungary	16	♀
Archieracium				
H. basifolium ALMQ.	SAMUELSSON	Stockholm		♀
H. reclinatum ALMQ.	»	»		♀
H. longimanum NORRL.	»	»		♀
H. pseudodiaphanum DT. ...	»	»		♀
H. subampliatum DT.	»	»		♀
H. lacerifolium ALMQ.	»	»		♀
H. triangulare ALMQ.....	»	»		♀
H. pellucidum LAEST.	»	»		♀
H. subulatidens DT.....	»	»		♀
H. lapponicum FR.....	»	Lapland	27	♂♀
H. rigidum HARTM. 1.	»	Stockholm		♀
H. rigidum HARTM. 2.	»	»		♀
Erigeron				
E. annuus (L.) PERS.....	SÖDERBERG	Hort. Berg.,		♂♀
E. ramosus (WALP.) B. S. P.	»	Stockholm		♂♀
Marsilia				
M. Drummondii A. BR. (var. *tomentosa*)		Lund Bot. Gn.		♂♀

Dr. H. DAHLSTEDT, Stockholm, and Dr. H. HANDEL MAZZETTI, Vienna. The material obtained from them has been taxonomically determined. Plants collected by the writer during excursions in 1930—1932 have been determined to the group, to a small extent to the individual apomict, in that case by Dr. HAGLUND. Some *Taraxacum* apomicts were obtained from the Rev. C. PERSSON, missionary, Jarkend, others were procured in the annual seed exchange by Lund Botanical Garden. The *Hieracium* apomicts examined (except *H. lapponicum*), which were fixed during a journey in the Stockholm district in 1934, have been determined by Prof. SAMUELSSON. The two species of *Erigeron* are fixed by Mr. O. GELIN, Stockholm, at Hortus Bergianus and are determined by Mr. E. SÖDERBERG, Stockholm.

Various methods of fixation have been employed. At first Carnoy's fluid with chloroform, according to ROSENBERG's method, was used. Owing to the complicated procedure of staining with gentian violet, which, it is true, gave exceedingly beautiful pictures, I went over to Navashin's chrom-formol-acetic solution, in the beginning without any preparatory fixation. During the last two years, however, preparatory fixation in Carnoy has invariably been made. Such a preparatory fixation for a few minutes gives considerably better results. Bouin's picric acid solution (modified by Allan), also with preparatory fixation, gave excellent results in the majority of cases. La Cour's and Fleming's fixatives, containing osmic acid, have also been used but the results were not quite so good.

The stain employed has almost exclusively been gentian violet, in the beginning of the investigations haematoxylin was also used. The sections have varied in thickness from 7 μ to 20 μ. The most suitable thickness was found to be 13—14 μ. Bleaching has occasionally been performed with hydrogen peroxide before staining.

The preceding table includes most of the apomicts examined with respect to the course of the meiosis. The chromosome numbers in root-tips have been ascertained in many more cases, but they are not included here. A special investigation will deal with the cyto-systematic results arising from the chromosome numbers.

3. THE CYTOLOGY OF TARAXACUM AND FEMALE ARCHIERACIUM.

A. PREVIOUS INVESTIGATIONS OF THE DEVELOPMENT OF THE MACROSPORES IN TARAXACUM.

Studies on this subject have been made by MURBECK (1904), JUEL (1905), ROSENBERG (1909), SCHKORBATOW (1912), OSAWA (1913),

STORK (1920), SEARS (1917, 1922), GUSTAFSSON (1934 a, 1935) and by PODDUBNAJA-ARNOLDI and DIANOVA (1934).

JUEL's paper is the fundamental one for the conception of the macrospore formation. In this work he shows two different kinds of diakineses, an early one with contracted chromosomes followed by another in which the chromosomes are elongated and plainly split lengthwise. According to JUEL, the chromosomes are again contracted at the following metaphase and are almost round or square in shape. Then occurs the longitudinal division and the two daughter nuclei obtain the zygoid chromosome number. Contrary to the case in related sexual species the chromosome threads in the apomictic form do not pair at prophase, and in the early diakinesis with contracted chromosomes they are invariably univalent.

Seen in the light of ROSENBERG's discovery of the restitution nuclei and the two modes of division I have shown to occur in *Taraxacum* (homotypic and pseudo-homotypic metaphases), an interpretation of JUEL's pictures will be an easy matter. The slender diakineses with long split chromosomes are, as ROSENBERG assumed (1917, 1927), nothing but restitution nuclei. The metaphase, which JUEL assumed to be a sequel of this diakinesis and which would again obtain round or square chromosomes, is a pseudo-homotypic metaphase. The true homotypic division is of course much more rarely seen in the prepared material and was therefore overlooked by JUEL. His pictures thus show: 1—6 prophases, 7—11 true diakineses, 12 a transition to metaphase (note the large number of chromosomes!), 13—15 restitution nuclei after a heterotypic metaphase or anaphase, 16—17 semi-heterotypic metaphase, 18 a transition to pseudo-homotypic metaphase, 19 and 20 two such metaphases, and finally 21 exhibits a pseudo-homotypic or homotypic anaphase.

SCHKORBATOW's pictures show: Plate 1, Figs. 6 and 7 two diakineses with respectively 24 and 17 evidently unpaired chromosomes, Figs. 8 and 9 two restitution nuclei with interkinetic chromosomes and Fig. 10 possibly a homotypic metaphase.

OSAWA's investigations confirm these interpretations. He points out two kinds of diakineses and a following metaphase, which also in his picture resembles a pseudo-homotypic metaphase. After the synaptic contraction the zygoid number of unpaired chromosomes is formed. In contradistinction to *T. platycarpum* no parasyndesis has taken place between different chromosome threads, thus zygotene pairing or chiasma formation has been omitted. Figs. 64—68 show

prophases, Fig. 69 a diakinesis, Fig. 70 a restitution nucleus, Fig. 71 probably a pseudo-homotypic metaphase and Fig. 72 a homotypic or pseudo-homotypic anaphase.

STORK establishes the manifest singleness of the »spireme threads» in the prophase of E.M.C. »If it is a double thread, the two halves are so intimately merged as to be indistinguishable» (1920, p. 207). At diakinesis the chromosomes are separated from one another and lie scattered over the whole of the nuclear cavity. STORK, in conformity with JUEL's interpretation, believes that after this stage the nucleus stretches and that the chromosomes assume the homotypic appearance mentioned by JUEL and OSAWA. Then the chromosomes are again shortened. »The chromosomes again return to an isodiametric form and appear to be smaller and possibly denser bodies than when they first assumed this form» (p. 208). This last stage is obviously nothing but the pseudo-homotypic metaphase. Further, he writes: »The chromosomes are at first loosely scattered over the entire spindle, but soon move toward the equatorial plane and are there arranged in quite regular order». This is exactly the description I have given of this type of division. — Finally, Fig. 16 probably shows — the chromosomes more elongated — a homotypic metaphase as a result of a restitution nucleus.

SEARS disagrees with JUEL's interpretation of the elongated diakinesis as a stage following normal diakinesis. According to SEARS »the elongated nucleus is a member of a distinct sequence» (1922, p. 320).

Further, he criticizes the interpretation of JUEL and OSAWA that the chromosome threads in the *Taraxacum* apomicts are single, as opposed to the case in the related sexual forms, which undoubtedly exhibit a parasyndetic arrangement. He states, instead, that he was able to find 13 pairs of pro-chromosomes, and that the univalents at diakinesis (in the female organs) arise by »the lateral refusion of the two halves previously split apart». For he is of opinion that »the thread entering synizesis shows in places a doubleness unexplainable at present. The thread emerging from synizesis becomes very evenly distributed through the nucleus, and then shows what is interpreted as non-simultaneous splitting» (p. 316).

Although this interpretation, like TAHARA's discovery in *Erigeron*, points to a zygotene pairing which is resolved at diakinesis, SEARS's pictures and his description are, however, so indistinct that no definite conclusion can be drawn. Owing to the fact that he does not disting-

uish the development of the pollen and the embryo-sac, which he himself admits differs in certain respects (pp. 318 and 319), he has been unable to throw light on the phenomena. Further, he considers that the stages, which according to ROSENBERG's studies of *Hieracium* and the present writer's investigations in *Taraxacum* are only interkineses, are amitoses which cause sterility.

Certain facts in his investigations are, however, of great importance. Thus, he established that no chromosome pairing occurs in the diakineses of the female organs, that only types B and D appear in the female organs (i. e. most closely resembling pseudo-homotypic divisions and restitution nuclei at interkinesis, the latter, in his opinion, synonymous with amitoses), and that tetrads have never been observed in the female organs: »Inspection of hundreds of embryo sacs failed to disclose tetrad formation» (p. 318).

GUSTAFSSON (1934 a, 1935) showed the occurrence of two entirely different modes of division in the E.M.C:s. One is the formation of restitution nuclei, which has been known for quite a long time and was correctly interpreted by ROSENBERG as early as 1917. The other method of division is the formation of a pseudo-homotypic plate, i. e. the univalents move actively towards the equatorial plane and divide there lengthwise. In both cases dyad formation occurs.

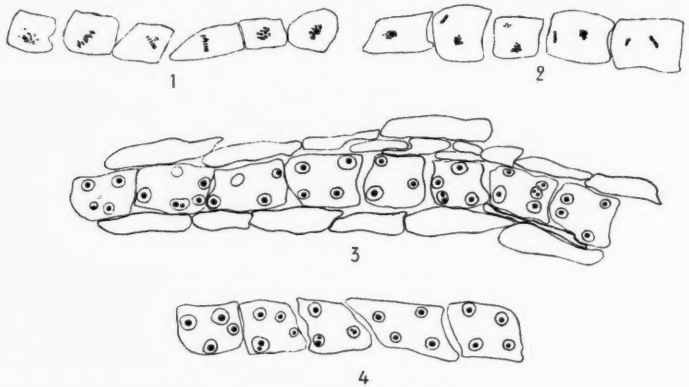
Finally, PODDUBNAJA-ARNOLDI and DIANOVA (1934) investigated the male meiosis in a number of sexual and apomictic biotypes. Their studies of the later course of the embryo-sac formation, to which I have paid no attention, should form a valuable complement to the studies mentioned above. The most significant result of their investigation, however, was the demonstration (p. 37) of the stability of parthenogenesis in *Taraxacum*. »Neben der Bildung von Dyaden bei den parthenogenetischen Biotypen haben wir kein einziges Mal die Bildung von Tetraden, Triaden u. s. w., überhaupt keine Abweichungen in der Dyadenbildung bemerken können.»

B. TARAXACUM.

T. fulvum RAUNK. Figs. 5—13. No pollen is ever formed. Loculi with P.M.C:s arise however, in which typical meiosis occurs. After the homotypic metaphase and the appearance of the tetrad nuclei, the P.M.C:s degenerate. Figs. 1—4 illustrate loculi in *T. Nordstedtii*, which also has the same type of development. The P.M.C:s are not round but retain the angular appearance and often lie close together. A similar condition has been described by ROSENBERG in *H. excellens*

(1917, p. 153). In 1927 ROSENBERG, and later BERGMAN (1935 a), assumed that in biotypes of *Archieracium*, where the P.M.C:s are not rounded but lie close together and have the same shape as here, the meiosis took place earlier than in sexual biotypes. The possibility of a physiological disturbance in the development of the P.M.C:s in *Hieracium* is not excluded.

Meiosis in *T. fulvum* is characterized by an intense formation of gemini. Solitary quadrivalents may occur (Fig. 5) and also trivalents. A noteworthy feature is the high degree of terminalisation and, associated with this, the small number of interstitial chiasmata, which, when they do occur (in accordance with DARLINGTON's theory), require

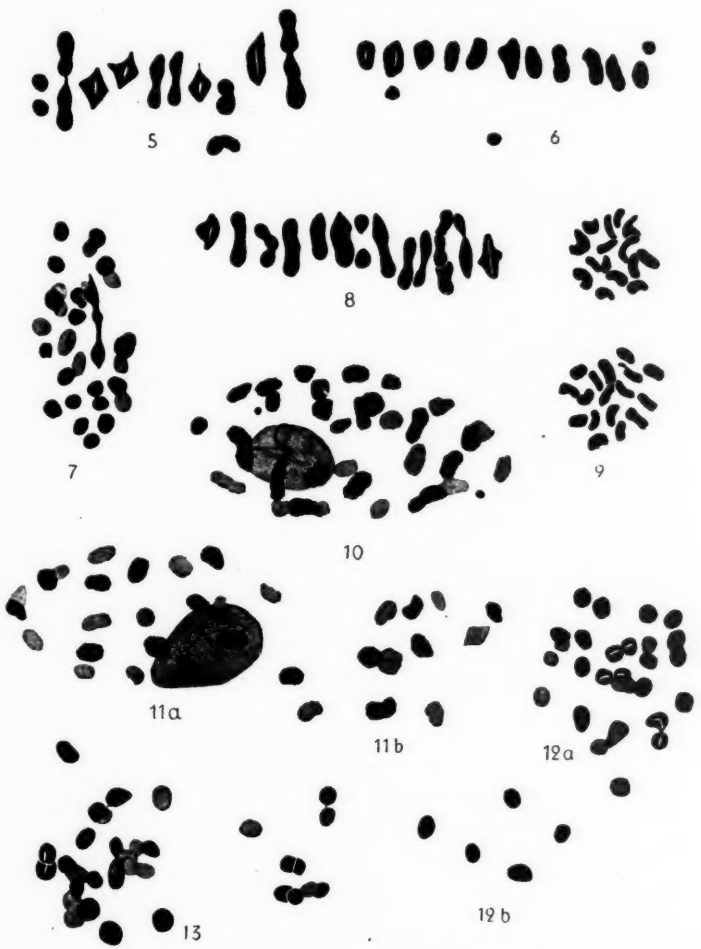


Figs. 1—4. *T. Nordstedtii* DT. P.M.C. — 1. 1st metaphase. — 2. 2nd metaphase. — 3—4. Pollen loculus at the tetrad stage. — About 400 ×.

a longer time for their resolution than the terminal chiasmata (Fig. 7). Univalents are formed in varying numbers.

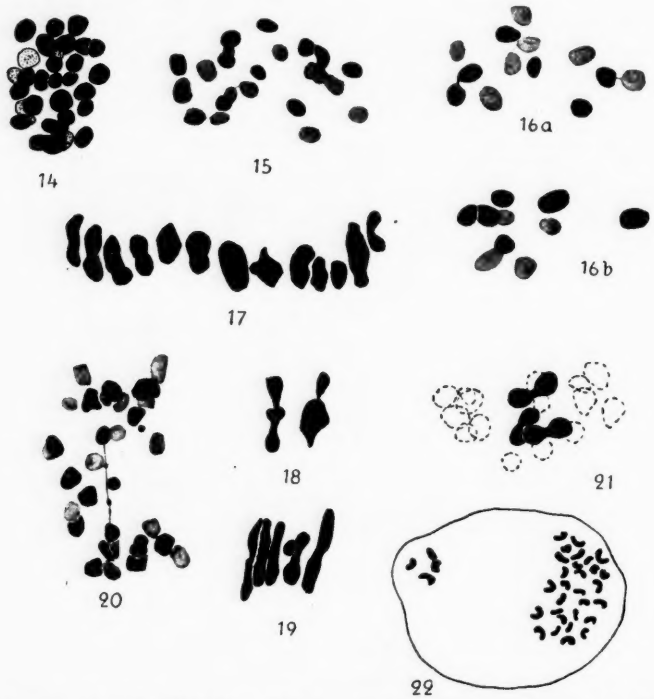
As in the case of *T. Nordstedtii* and *Hieracium umbellatum* f. *apomicta* (BERGMAN) autoploidy is most likely. Here, however, spontaneous chromosome doubling in an allodiploid biotype probably has occurred. The occurrence of the polyvalents and the univalents are explained by assuming that there is a deficient but nevertheless existing slight homology between the two genomes of the diploid original type.

A large number of diakineses have been studied in the E.M.C:s. All of them showed univalence. »Synaptic contraction» was not observed. The metaphases contain varying degrees of pseudo-geminus formation. The highest number of associations found amounts to 6—8. In one case $1_{III} + 6_{II} - 4_{II}$ was observed. One restitution nucleus



Figs. 5—13. *T. fulvum* RAUNK. 5—9. P.M.C:s. 10—13. E.M.C:s. — 5. 1st metaphase with two quadrivalents and several terminalized bivalents. — 6. 1st metaphase with most gemini terminalized. — 7. 1st anaphase with one »lagging» interstitial bivalent. — 8. Complete 1st metaphase with one trivalent and some interstitial bivalents. — 9. 2nd metaphase. — 10—11. Diakineses with complete univalence (fragments ?). — 12. The formation of a pseudo-homotypic metaphase with probably three secondary associations. — 13. 1st metaphase in two sections with 6—8 secondary associations. One in the middle of 13 left section, stretched in the longitudinal direction of the spindle, behaves like a terminalized eugeminus. — 2800 ×.

and one pseudo-homotypic metaphase in process of development have been recorded. In 24 ouf of 29 dyads the basal dyad cell had developed, in 1 the apical cell. One or two cases of binucleate embryo-sacs, composed of the two first daughter-nuclei have been observed. In one case there *possibly* occurred a triad.



Figs. 14—22. 14. *T.* *1930:685.* E.M.C. 15—16. *T. tenuilobum* Dt. E.M.C:s. 17—22. *T. 1930:302.* P.M.C:s. — 14. Pseudo-homotypic metaphase. — 15. Metaphase-anaphase with 4 associations. — 16. Metaphase-anaphase with about three associations. — 17. Metaphase with 13 bivalents. — 18. One trivalent and one bivalent with interstitial chiasma. — 19. Four bivalents and one trivalent. — 20. Anaphase with a lagging trivalent. — 21. Metaphase with three gemini. — 22. 2nd metaphase. The large plate probably due to incomplete restitution. — 14—21, 2600 ×. 22, about 1500 ×.

T. ruberulum Borgw. et Dt. No P.M.C:s were examined. A few diakineses with 23—25 unpaired elements were observed in the E.M.C:s.

T. 1930:685. Fig. 14. This biotype was obtained in progenies of a triploid *Erythrospermum* apomict. It is probably an intermixture,

the tetraploid number indicates this. Only a few divisions in the female organs have been examined, which were pseudo-homotypic metaphases in process of development. Fig. 14 shows such a metaphase without any secondary associations. In another case 3 secondary associations were observed.

T. tenuilobum DT. Figs. 15—16. A previously published investigation of P.M.C:s showed a varying degree of pairing, sometimes with as many as 8 gemini. In 20 P.M.C:s out of 30 from 1 to 3 interstitial chiasmata were observed (GUSTAFSSON, 1934 c). In that paper this apomict was erroneously named *T. brachyglossum.*

Several diakineses, but not of good condition, have been studied in the E.M.C:s. In the majority of cases the chromosomes were evidently unpaired, a few doubtful cases showed threads between solitary univalents.

The metaphases and anaphases were on the whole good. Figs. 15—16 show 2 such stages with evident associations. Terminal threads (in my opinion the stretched pellicles of the chromosomes) connect some of them. Semi-heterotypic metaphases without any secondary associations have also been observed.

T. 1930:287. Fig. 118. Only meiosis in the female organs has been examined. Semi-heterotypic divisions at diakinesis to metaphase have been observed, also restitution nuclei (1935, Fig. 53) and pseudo-homotypic metaphases. 44 dyads but no triads or tetrads have been recorded. The formation of pollen is noteworthy inasmuch as in 13 % of 393 P.M.C:s studied in the tetrad stage monads were present. The cause of this condition is unknown. Sometimes the cells, however, contain four nuclei, between which no wall has been formed.

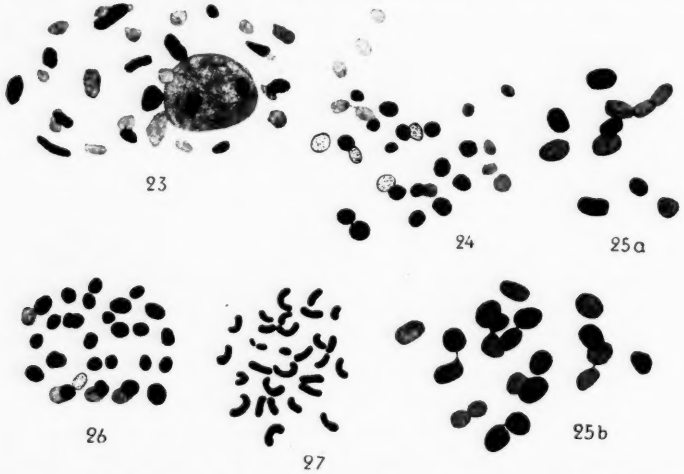
T. 1930:302. Figs. 17—44. This biotype exhibits in the P.M.C:s a series of degenerative phenomena, the explanation of which is of value. Table 2 shows the number of cells of the tetrad stage in the P.M.C:s.

TABLE 2. *Number of »Tetrad Cells» in 1930:302.*

1	2	3	4	5	6	7	8	9	10	11	12	
1?	36	35	176	19	16	6	7	1	1	1	1	= 300

As far as the P.M.C:s containing 8—12 nuclei are concerned, this polyad formation is due to the fact that no wall-formation has taken place in an early stage between the P.M.C:s. Of 303 P.M.C:s studied 24 consisted of 2 cells without wall-formation and one P.M.C. consisted of 3 cells. If a corresponding number is deducted from the above Table

the percentage of pentads and hexads (heptads) will still be rather high, approximately 12 %. This is perhaps due to a peculiarity in the accomplishment of metaphase observed only in this apomict. In the metaphase position of the bivalents membranes are occasionally formed around solitary gemini or clusters of gemini so that a number of nuclei arise already here. Figs. 35—36 show examples of this. In the following metaphase the spindles (or earlier the nuclei) probably often fuse, for the number of homotypic spindles in each cell is rather low. In 146 P.M.C:s examined in homotypic division in 33 cases there occurred one spindle, in 104 cases two spindles and only in 9 cases were there



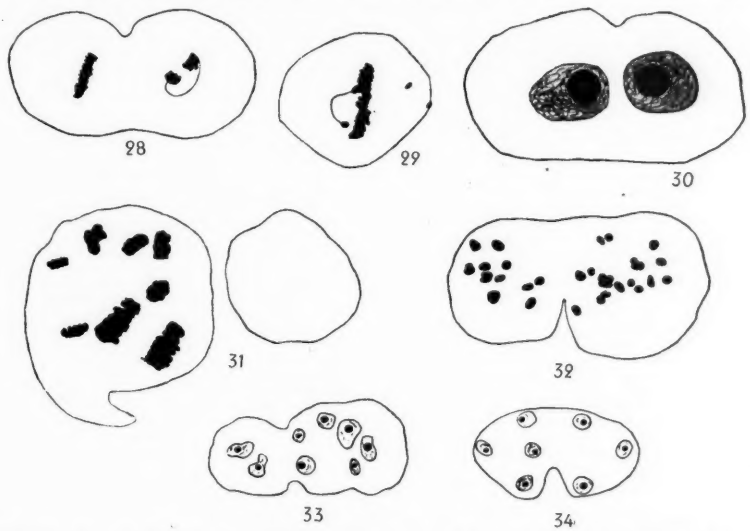
Figs. 23—27. *T. 1930:302.* E.M.C:s. — 23. Diakinesis with complete univalence. — 24. Metaphase with one probable association. — 25. Metaphase with at least one pseudo-trivalent and 7 pseudo-bivalents. — 26. Pseudo-homotypic metaphase. — 27. Homotypic division. — 2800 ×.

more than two spindles. This formation of nuclear membrane is degenerative, for degeneration in the formation of restitution nuclei is very pronounced.

Besides this curious formation of membrane already at first metaphase there arise at anaphase pictures of a peculiar appearance (Figs. 37—42). They are undoubtedly restitution nuclei. In a following chapter the essense of the restitution formations will be treated more closely (p. 83), here it is only necessary to point out that the nuclear membranes, which arise around and join isolated chromosomes to the two anaphase plates, evidently arise in the spindle, not

at its periphery, and that their extent is to a certain degree of an arbitrary character. Such restitution nuclei have never been observed in the female organs. Fig. 43 shows a homotypic plate after the disappearance of a circular nuclear membrane as in Fig. 38 *a*. In Fig. 44 the restitution nucleus has not developed in spite of the fact that a chromosome loop connects the two daughter nuclei. In Fig. 38 *b* a wall has been formed around two clusters of gemini (?) while all the other chromosomes have been enclosed in a common membrane.

The formation of gemini in P.M.C:s is variable, the smallest num-



Figs. 28—34. *T. 1930:302.* P.M.C:s. — 28. 2nd division. No wall between the two P.M.C:s. — 29. Normal P.M.C. at the same magnification. Restitution nucleus. — 30. No wall between the two cells. Resting stage before division. — 31. To the left a P.M.C. with 4 homotypic anaphases, to the right a normal P.M.C. — 32. No wall between the two cells. 1st metaphase-anaphase. — 33. Two or three »fused» P.M.C:s. — 34. No wall between the two cells. Tetrad stage. — 28—32, about 900 ×. 33—34, about 600 ×.

ber of gemini observed is three while the largest number recorded is thirteen. Trivalents occur not infrequently, but in spite of the tetraploid number no quadrivalents have been found.

The state of things in the E.M.C:s demonstrates completely the two types of division occurring in *Taraxacum*. Figs. 26 and 27 illustrate two plates, situated close to each other in a cross-cut head, but in such a manner that the cell with plate 27 was in the older ovule. Of the

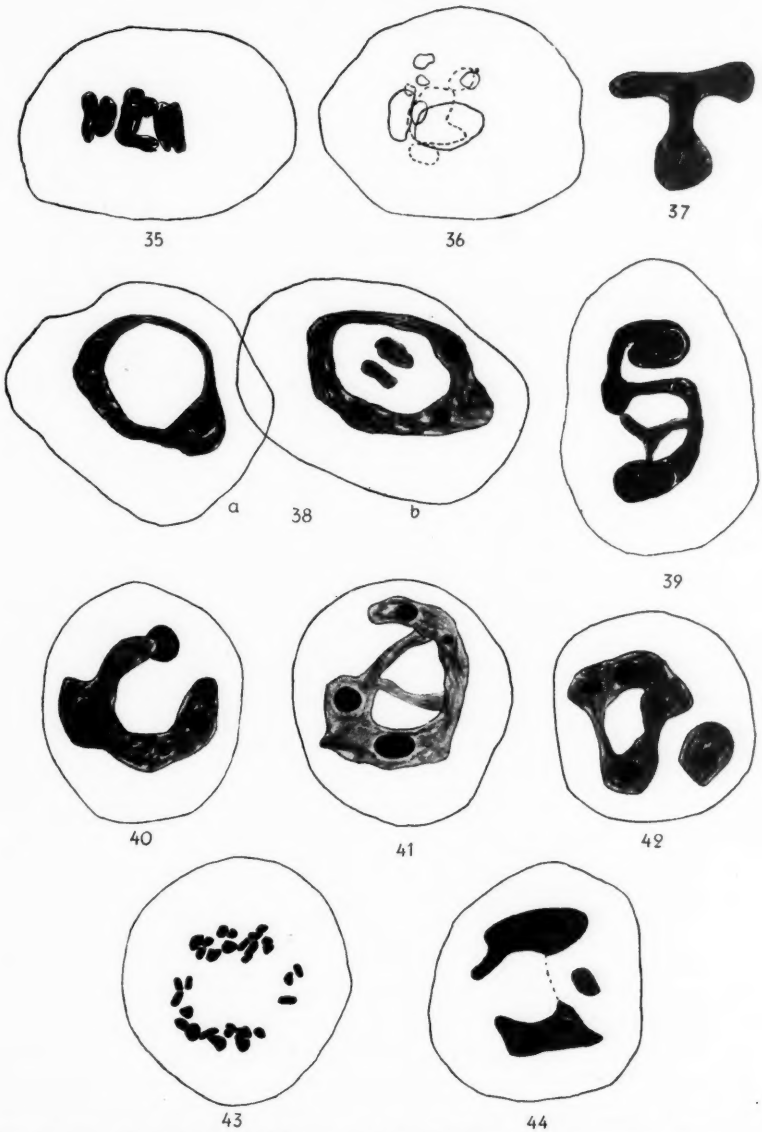
32 chromosomes in Fig. 26, 25 are lying entirely in the same plane, above and below them 6 and 1 respectively. Hence the pseudo-homotypic metaphase is here almost fully developed. The chromosomes, all of which appear to be unpaired, have a distinctly heterotypic appearance, and the difference between this plate and plate 27 is striking. The location of the two stages in the head is that expected. While the pseudo-homotypic metaphase is only a continuation of the heterotypic, the chromosomes present in the homotypic stage must have previously passed through heterotypic anaphase and interkinesis. (Cp. GUSTAFSSON, 1934 a, p. 270).

T. 1930:719. Fig. 45. Only P.M.C:s have been examined. Only semi-heterotypic metaphases occur (few divisions observed). Restitution nuclei are formed at the rate of 25 %.

T. 1930:653. Figs. 46—48. Only the development in the E.M.C. has been studied. The figures show the course of the homotypic division. In Fig. 46 an interkinesis is seen in the last period of the resting stage. The chromosomes appear divided lengthwise with the halves repelling each other. In the second metaphase the chromosomes again assume their usual appearance, that is, the chromatids lie close to one another along their entire length (47, the ovule transversely cut). The longitudinal fissure appears, however, quite plainly in less deeply stained material (Fig. 48). Prophases without any »synaptic contraction», solitary diakineses, numerous interkineses, some pseudo-homotypic metaphases and, finally, dyads have been observed. Of 16 dyads 11 had the basal dyad cell developed and 3 the apical cell.

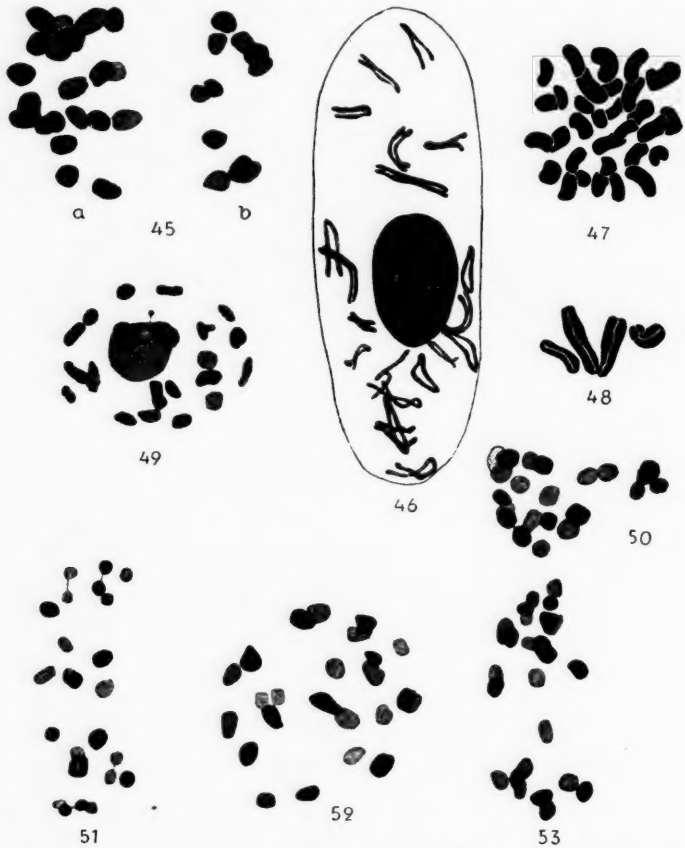
T. croceum DT. In the few slides examined the P.M.C:s exhibit isolated cases of lagging univalents (in 3 out of 28 anaphases). Judging from the small amount of material, the pairing is rather high, solitary trivalents and even tetravalents occur. Consequently there appear only a small percentage of dyads (3 %). The rather high rate of polyad formation (29 %) shows that lagging univalents should occur to a greater extent than indicated by the anaphases observed. In 5 out of 24 homotypic anaphases lagging chromatids occurred, in 4 of them the same number in both spindles. Only dyad stages were observed in the E.M.C:s. One case with uncertain dyad or tetrad formation was met with. Of 11 dyads 9 had the apical cell developed.

T. litorale RAUNK. Figs. 49—53. No pollen is ever produced, for the P.M.C:s degenerate before the nuclei have passed out of the resting stage. The E.M.C. has been subjected to a careful examination as far as the metaphase and the anaphase are concerned. One recorded diakinesis



Figs. 35—44. *T. 1930:302.* P.M.C:s. — 35—36. The formation of membranes around the solitary gemini or groups of gemini. — 37. A restitution nucleus of a curious shape. — 38. Two P.M.C:s with ring-shaped restitution nuclei. In addition, in *b* two small nuclei. — 39. One incomplete restitution nucleus and one small nucleus. — 40. Incomplete restitution nucleus. — 41. Restitution nucleus. — 42. Incomplete ring-shaped nucleus. — 43. A restitution nucleus at 2nd division. — 44. A small chromatin thread between the two daughter nuclei. — About 2000 ×.

contained 23—24 unpaired chromosomes (Fig. 49, here only 23 chromosomes are drawn). Fig. 52 illustrates an early metaphase in which



Figs. 45—53. *T. 1930:719.* P.M.C:s. 46—48. *T. 1930:653.* E.M.C:s. 49—53. *T. litorale* RAUNK. E.M.C:s. — 45. Semi-heterotypic metaphase. — 46. A restitution nucleus at early 2nd prophase. — 47. Homotypic metaphase. — 48. Some homotypic chromosomes. — 49. Diakinesis with 23 univalents. — 50. Incomplete metaphase with at least two associations. — 51. Anaphase with 4 associations. — 52. Early metaphase. — 53. Semi-heterotypic metaphase-anaphase. — 2800 ×.

the nuclear membrane and the nucleolus have just been resolved. Two chromosomes lie close to each other in the same plane, but not in the longitudinal direction. Whether they would later form a secondary

association is impossible to decide. In Fig. 51 are seen four associations where there cannot be any doubt as to the existence of the threads in the longitudinal direction. Restitution nuclei, but no sure pseudo-homotypic divisions, have been observed.

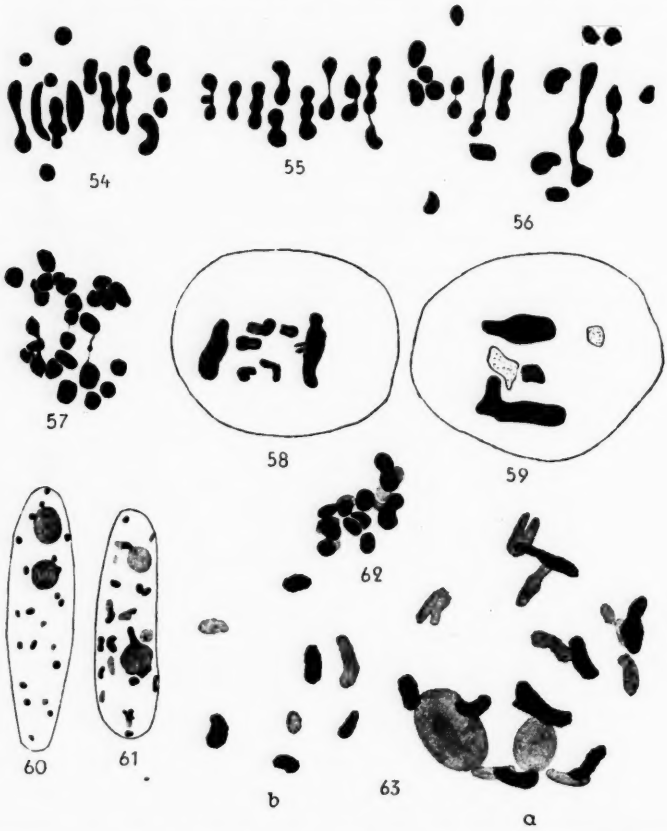
T. sublaeticolor DT. See GUSTAFSSON, 1934 a, p. 261 and Figs. 30—31. In addition to the pseudo-homotypic metaphases reproduced there some diakineses in E.M.C:s with 24—26 unpaired chromosomes have been observed, also heterotypic and homotypic metaphases and 4 dyads.

T. melanthoides DT. Figs. 54—59. Of this form only P.M.C:s have been examined. An interesting feature is the large number of gemini, occasionally amounting to more than 8 but now and then being less. In contradistinction to the condition in *T. praestans* (GUSTAFSSON, 1934 c) the lowest number of gemini observed however is 7. Fig. 54 shows 10 gemini, 3 or 4 of which have certainly interstitial chiasmata. No trivalent was present here. In Fig. 55, on the other hand, a trivalent can be seen on the extreme right. The number of gemini could not be determined here with certainty, possibly the two gemini above one another as No. 4 from the left are only a bivalent or trivalent. At least four (one of which is the trivalent) possess interstitial chiasmata. In Fig. 56 a trivalent is present — the large formation on the right — in addition to which there are at least 7 bivalents, three of which have already been separated into their constituents. Probable interstitial—subterminal chiasmata occur. The interstitial chiasmata, as usual, cause a delay in the separation of the chromosomes. Fig. 57 shows an anaphase with one interstitial, one probably subterminal and one terminal chiasma. A result of the incomplete pairing is the larger or smaller number of univalents (Table 3), which in this biotype, as in others with a high rate of pairing at anaphase, often move towards the equatorial plane, where they divide lengthwise. As I shall point out later on (p. 90), this condition is an indication that the period of time diakinesis — anaphase in forms with pairing is longer than the corresponding period in biotypes with semi-heterotypic divisions. Late anaphases show a high percentage of small nuclei. In spite of the univalence it is very seldom that restitution nuclei and their results, dyads, are formed.

TABLE 3. *Number of Univalents at Metaphase in T. melanthoides* DT.

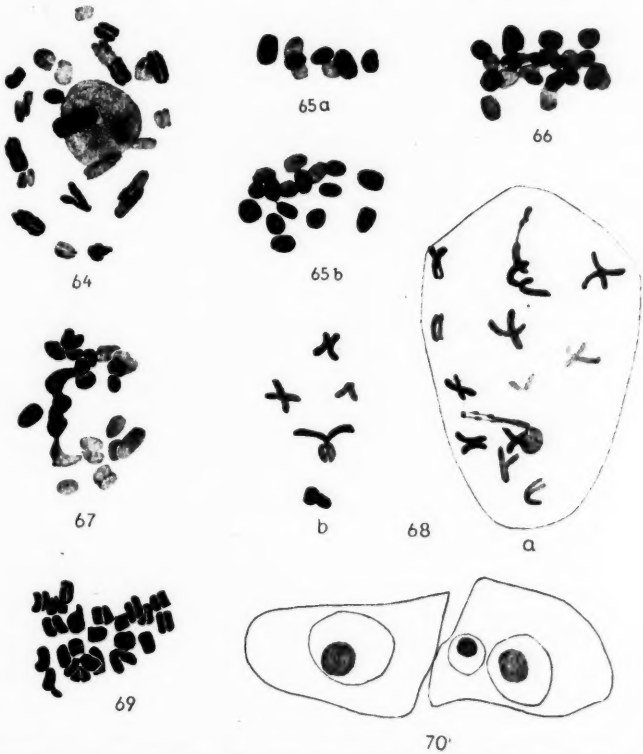
Number of univalents	3	4	5	6	7	8	9	10
» » cases	9	20	16	15	11	6	2	2 = 81

T. retroflexum LINDB. fil. Figs. 60—62. Only E.M.C:s have been examined. A large number of restitution nuclei have been observed, two of which are shown in Figs. 60 and 61. The chromosomes in



Figs. 54—63. 54—59. *T. melanthoides*. P.M.C:s. 60—62. *T. retroflexum* LINDB. fil. E.M.C:s. 63. *T. Ekmani* DT. E.M.C:s. — 54. 1st metaphase with 10 gemini, 3—4 of which have interstitial chiasmata. — 55. 1st metaphase with one trivalent and 7—8 bivalents. At least 4 gemini with interstitial chiasmata. — 56. Early anaphase. Some bivalents already separated. Probably one trivalent, in addition to 7 bivalents. — 57. Anaphase. One interstitial bivalent »lagging». — 58. Anaphase with 8 lagging and dividing univalents. — 59. The formation of small nuclei. — 60—61. Restitution nuclei, probably before the resting stage. Note their stretched shape. — 62. The formation of a pseudo-homotypic metaphase. Two associations visible, more or less in the longitudinal direction of the spindle. — 63. Diakinesis with 24—25 univalents. — 54—57, 62—63, 2800 ×. 58—59, 60—61, about 1500 ×.

Fig. 60 still possess the heterotypic appearance; most likely the restitution nucleus has just been formed. Neither does Fig. 61, where the chromatids have however already begun to separate, show a stage



Figs. 64—70. *T. laeticolor* Dt. E.M.C:s. — 64. Diakinesis with 24 univalents, two of them in the same plane. Chromatids plainly visible. — 65. Pseudo-homotypic division. One association. — 66. Pseudo-homotypic division. 22—24 univalents were visible. — 67. Anaphase with one probable pseudotrivalent and one pseudogeminus. — 68. A restitution nucleus after interkinesis. The nucleolus is nearly dissolving. — 69. Homotypic division. Owing to the nucleus having been cut obliquely the chromosomes are not lying in the same plane. — 70. A dyad with three nuclei. — 64—69, 2800 ×. 70, about 1500 ×.

during or after interkinesis. Prophases, diakineses and pseudo-homotypic metaphases in process of formation (Fig. 62) have also been observed. In the fixed material, however, the dyad stages were those most numerously represented; not less than 94 have been recorded, 20

of which had the basal dyad cell developed, 12 the apical cell. No triads or tetrads were observed.

T. Ekmani DT. Fig. 63. Only two diakineses in the E.M.C:s have been observed, both however with evidently unpaired chromosomes. The low degree of dyad formation and the corresponding high degree of polyad formation in P.M.C:s indicate a comparatively extensive formation of bivalents.

T. laeticolor DT. Figs. 64—70. Of this form a large number of E.M.C:s have been examined. All stages have been observed. It has been possible to analyse prophases, and in early stages — corresponding to leptotene or zygotene — these show single chromosome threads spread over the entire nucleus. Thus no manifest »synaptic contraction» has been observed. The recorded diakineses are few in number, Fig. 64 shows a diakinesis in which all the chromosomes were unpaired — although double in structure owing to the pre-diakinetic division. Towards the top left hand corner there are, however, two chromosomes lying close to one another in the same plane. Whether this is an incidental occurrence, a secondary association already beginning or a result of zygotene pairing without any chiasma formation, is not possible to decide. They do not form any true geminus. The metaphases show a low rate of secondary associations. Fig. 67 shows an anaphase with a probable pseudo-trivalent plus an association between two chromosomes; Fig. 65 shows one or two associations in a pseudo-homotypic metaphase in the course of formation, while Fig. 66 shows the same stage as in Fig. 65 but without any secondary associations. A homotypic metaphase is drawn in Fig. 69. Owing to the ovule having been cut obliquely the chromosomes do not lie in the same plane.

Fig. 70 shows that disturbances *may* occur in the formation of dyads. The fixations of this biotype were made, however, as late as the end of October (1933) and therefore the irregularity may be due to that reason and may not occur spontaneously. Otherwise the dyad formation was always regular. Of 52 regular dyads recorded 16 had the basal dyad cell developed and 3 the apical cell.

In this biotype, too, two ovules were discovered with the homotypic and the pseudo-homotypic stages bordering on each other. In the older ovule there was a restitution nucleus, in the younger a pseudo-homotypic division. The formation of the homotypic metaphase thus requires a longer time than the formation of the pseudo-homotypic, owing to the fact that the chromosomes, as in the P.M.C., must pass

through an interkinetic stage in which the »chromosome individuality» disappears.

T. 1930:679. Figs. 71—73. The number of gemini in the P.M.C. varies within narrow limits, less than 5 or more than 7 have not been observed. As the counts were mostly made on incomplete or divided metaphase plates, the number is possibly calculated too low. Semi-heterotypic divisions were not found, neither were any trivalents. A noteworthy feature is the high degree of terminalisation. Solitary interstitial chiasmata were however observed. Of 55 P.M.C:s containing homotypic metaphases 51 consisted of at least two plates with spindles, one undoubtedly of a restituted plate. The number of restitution nuclei is thus in keeping with the facts given on p. 88; few in spite of the high univalent number.

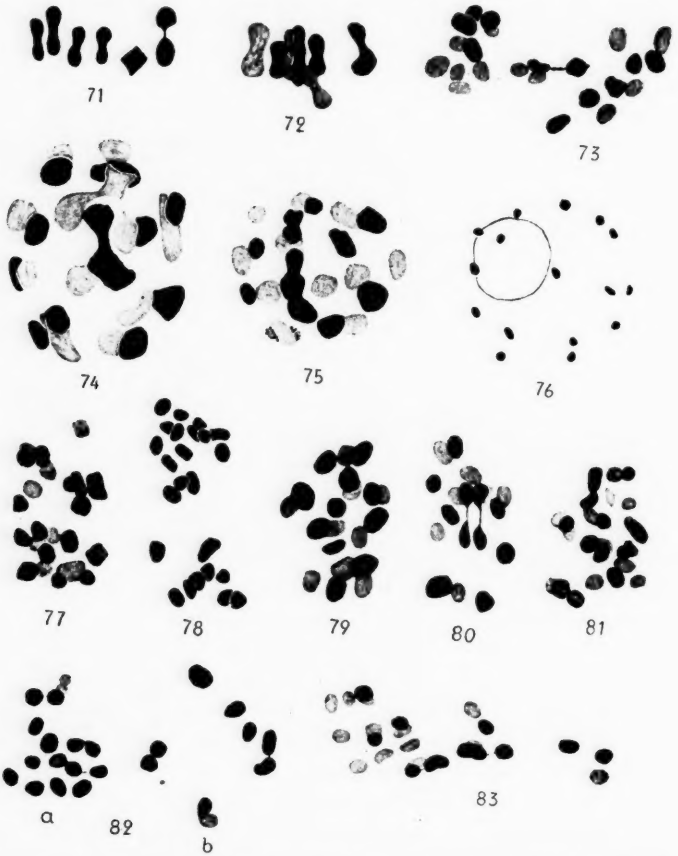
In the E.M.C:s some prophases and diakineses have been examined. One of the latter contained 24 unpaired chromosomes, another showed about 26.

T. 1929:5. Figs. 74—76. As already mentioned in a previous paper (1935, p. 9), this biotype seems to possess an increased frequency of gemini from diakinesis to metaphase. The material investigated is however rather small and re-examinations of the old material have disclosed a number of artefacts. Still, pro-metaphases in the P.M.C:s are excellent. The two pictures show two such pro-metaphases, each of them with one trivalent and one bivalent. Fig. 76 shows a diakinesis from the same loculus next to them. The rapid chromosome growth in connection with the reduction of the nucleolus is striking. In certain metaphases 6, 7, 9 gemini were found. Trivalents were also observed here. The exceedingly high polyad frequency (43 %, p. 87) may possibly indicate that the intense »formation of gemini» is associated with a wall-formation already at metaphase (?). Of 175 P.M.C:s in homotypic metaphase 57 contained one restituted group of chromosomes, 92 two groups, 27 three groups, 17 four groups and finally 1 five groups. Corresponding to the rather large number of restituted homotypic metaphases there is in the tetrad stage a dyad formation of 13 per cent.

In the E.M.C:s some prophases, diakineses with unpaired chromosomes and a pseudo-homotypic division have been recorded, in addition to a few dyad stages.

T. 1929:8. Figs. 79—80. Of this biotype a number of semi-heterotypic divisions in P.M.C:s have been studied. In one metaphase

two gemini have been observed, both terminalized. No E.M.C:s have been examined.



Figs. 71—83. 71—73. *T. 1930:679.* P.M.C:s. 74—76. *T. 1929:5.* 77—78. *T. 1929:19.* P.M.C:s. 79—80. *T. 1929:8.* P.M.C:s. 81. *T. haematopus* Dt. E.M.C. 82—83. *T. praestans* Lindb. fil. E.M.C:s. — 71. Metaphase with 6 bivalents, all terminalized, one with two chiasmata. — 72. Metaphase with 7 gemini. — 73. Anaphase with one »lagging» subterminal bivalent. — 74—75. Prometaphases with one trivalent and one bivalent each. — 76. Diakinesis. Note the unequal size of the chromosomes in Figs. 74—76. — 77. Semi-heterotypic metaphase. — 78. Anaphase. — 79. Semi-heterotypic metaphase. — 80. Metaphase with two terminalized bivalents. — 81. Metaphase with two associations. — 82. A pseudo-homotypic division with at least 5 associations. — 83. Anaphase with one pseudo-trivalent (?) and 1—2 pseudo-bivalents. — 2600—2800 ×.

T. 1929:19. Figs. 77—78. In P.M.C:s of this biotype semi-heterotypic diakineses and metaphases as well as gemini have been observed. In diakineses and metaphases the number of gemini varies between 0 and 6.

T. 1930:181. Meiosis in P.M.C:s has already been described (1932 b). I have not been able to explain the causes of the increased number of chromosomes in certain P.M.C:s, all the more as the numbers were not only doubled or trebled but also increased by single entire genomes. Pre-meiotic disturbances must however be postulated. Wall-formation between the P.M.C:s was frequently missing. The gemini in normal metaphases with their varying degree of pairing were always terminalized.

T. haematopus DT. Fig. 81. In the E.M.C:s diakineses, metaphases and pseudo-homotypic divisions were observed. 0—1—2 associations occurred.

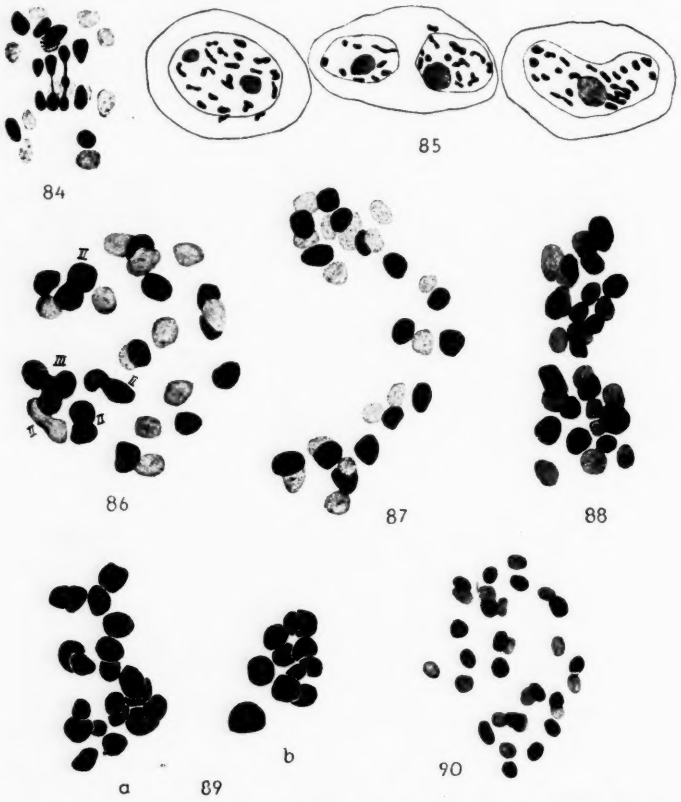
T. »Arjeploug 4». A somewhat varying number of gemini, up to 7—8 (— 9), occurs. Trivalents are frequently formed. Not more than two have been observed in the same cell. In one or two cases quadrivalents have also been recorded. In spite of this high rate of gemini formation no bivalents arise in the E.M.C:s (cp. GUSTAFSSON 1933, p. 532). In the E.M.C:s diakineses, anaphases and pseudo-homotypic divisions have been studied. In the paper cited I expressed the opinion that only pseudo-homotypic divisions occurred. Interkineses, which were then thought to be early diakineses, are however also met with.

T. Nordstedtii DT. See Figs. 1—4 and GUSTAFSSON, 1935.

T. maculigerum LINDB. fil. Semi-heterotypic diakineses and metaphases in the P.M.C:s are the most common. Pseudo-homotypic metaphases of varying appearance occur occasionally. (GUSTAFSSON, 1934 c).

T. praestans LINDB. fil. Figs. 82—83. The P.M.C:s most frequently exhibit semi-heterotypic divisions, but a certain high rate of gemini formation also occurs (more than 8). Correlated with the failure of pairing is the formation of secondary associations during the course of metaphase and anaphase (GUSTAFSSON, 1934 c). Later, E.M.C:s have also been examined. Fig. 82 shows a metaphase in two sections. Although the ovule in question was cut lengthwise there is probably a pseudo-homotypic division. As I have already pointed out (1934 a, p. 267) the position of the nuclear spindle varies in certain biotypes in the E.M.C. — In the same figure there appear at least 5 associations. The light-coloured formation at the top left hand corner is probably

an already divided univalent. — In Fig. 83 is seen an anaphase in which a trivalent-like association occurs in the centre. In the left anaphase plate there appears an association between two chromosomes of unequal



Figs. 84—90. P.M.C:s. 84—85. *T. palustre* coll. 86—89. *T. lanceolatum* POIR. 90. *T. balticum* DT. — 84. Metaphase with one interstitial and three terminalized bivalents. — 85. Two restitution nuclei. — 86. Prometaphase with one trivalent and 4 bivalents. — 87. Oblique anaphase. — 88—89. Anaphases. Note the laggards in 87—89. — 90. Semi-heterotypic division. — 2600 × (except 85, which is about 1200 ×).

size, the same phenomenon as that observed in the P.M.C:s. Homotypic metaphases have also been studied. Of 6 dyads, 1 had the basal cell developed and 3 the apical cell.

T. dissimile DT. See p. 38 and GUSTAFSSON, 1934 a. No pollen

is ever produced. Instead, loculi with a row of cells rich in nucleoli arise, and the P.M.C:s degenerate at an early stage.

T. pseudofulvum LINDB. fil. This biotype does not produce any pollen either. The P.M.C:s degenerate into tapetal cell-like formations. Three dyads in the E.M.C:s have been observed, in 2 of which the basal cell was developed.

T. palustre EHRH. coll. Figs. 84—85. Like *T.* ad *scaturiginosum*, this biotype differs from the Swedish *Palustria* apomicts in its triploid number. Only P.M.C:s have been examined. Meiosis is characterized by a high frequency of semi-heterotypic metaphases; solitary gemini are not rare, in one case as many as 6 were met with. Trivalents have been observed but never more than 1 in the same cell. A noteworthy and characteristic feature is the high rate of restitution nuclei (53 %, p. 87). These restitution nuclei have a more regular shape than is usual in the P.M.C:s. Many restitution nuclei develop a membrane at such an early stage that they resemble diakineses (Fig. 85, to the left hand). Pictures similar to ROSENBERG's, 1927, p. 320, occur. This regularity, which reminds one of the E.M.C:s, must certainly be due to the fact that the new nuclear membrane is formed on the margins of the spindle at the same time as or prior to the stretching (cp. p. 89). — 5 fragments were observed at meiosis. 2 of them were occasionally paired. No detailed analysis of their behaviour was made.

T. lanceolatum POIR. Figs. 86—89. Even as regards this biotype I was of opinion, based on my investigations made at that time (1935), that the number of gemini was perhaps increased by secondary association from diakinesis to metaphase. In that material, however, the metaphase plates, like those of *T. 1929:5*, were not fixed so well as the prometaphases and therefore only the number of gemini in the latter can be regarded as quite certain. As only 11 diakineses, 4 prometaphases and 9 more or less good metaphases have been examined, the observed increase is perhaps nothing more than an incidental variation. I therefore do not venture, any more than I did in my paper cited above, to maintain that the »increase» is caused by secondary association.

A more significant feature is the failure of dyad formation in spite of the large number of laggards formed in the anaphases (Figs. 87—89). Cp. p. 88. The anaphases have frequently the curved appearance shown in Fig. 87. The middle part is thin, owing to the stretching of the spindle. This condition has not been discovered in any other apomict.

T. balticum Dt. Figs. 90—94. No pollen is produced but the P.M.C:s undergo division and do not degenerate until after the homo-

Figs. 91—100. 91—94. *T. balticum* Dt. E.M.C:s. 95—96. *T. ecorniculatum* Hagl. P.M.C:s. 97—99. *T. ceratophorum* Ledeb. coll. 100. *T.* ad *scaturiginosum* Hagl. — 91—92. Diakineses with complete univalence. Probably also fragments. — 93. Homotypic metaphase in side view. — 94. Pseudo-homotypic metaphase in course of formation. — 95. Diakinesis with 1—2 quadrivalents, 10—12 bivalents (in the latter case two bivalents are secondarily associated) and 4 univalents. — 96. Two trivalents and 4 quadrivalents from different nuclei. — 97—99. Pseudo-homotypic division in progress. — 100. Semi-heterotypic metaphase with 23 univalents. — 2600—2800 ×.

typic division. Diakineses and metaphases were semi-heterotypic; no bivalent formation has been observed.

Many excellent diakineses in the E.M.C:s have been studied. The fact that all of them showed complete univalence is not remarkable in itself, as even the P.M.C:s contain semi-heterotypic divisions. In later stages, however, solitary associations have been discerned; Fig. 94 shows a pseudo-homotypic division with such an association. Fig. 93 illustrates a homotypic metaphase. The difference between the two stages is striking. No »synaptic contraction» was discovered in the prophases. 3 dyads were recorded, 2 of which contained cells of equal size, the third, on the other hand, had the apical cell developed.

T. ad *scaturiginosum* HAGL. Fig. 100. Only E.M.C:s have been examined. Four diakineses with unpaired chromosomes have been observed. In two of them the number could not be determined for certain (22—24 univalents). There also occurred a few semi-heterotypic divisions with probable secondary associations.

T. ecorniculatum HAGL. in sched. Figs. 95—96. In conformity with the tetraploid number this apomict exhibits to a large extent solitary tetravalents and trivalents in the P.M.C:s. Fig. 95 shows a completely analysed diakinesis: $2_{IV}(?) + 10_{II} + 4_{I}$. The metaphases showed a similar arrangement. Thus, one such metaphase contained 1 quadrivalent and 10 bivalents, another 10 bivalents, a third the same number and a fourth 1 quadrivalent, 1 trivalent and 10 bivalents. When this apomict was examined no direct records were made with respect to the terminalisation but the recorded plates seem to have a high degree of terminalisation, which is also confirmed by the bivalents in Fig. 95 and some of the multivalents in Fig. 96.

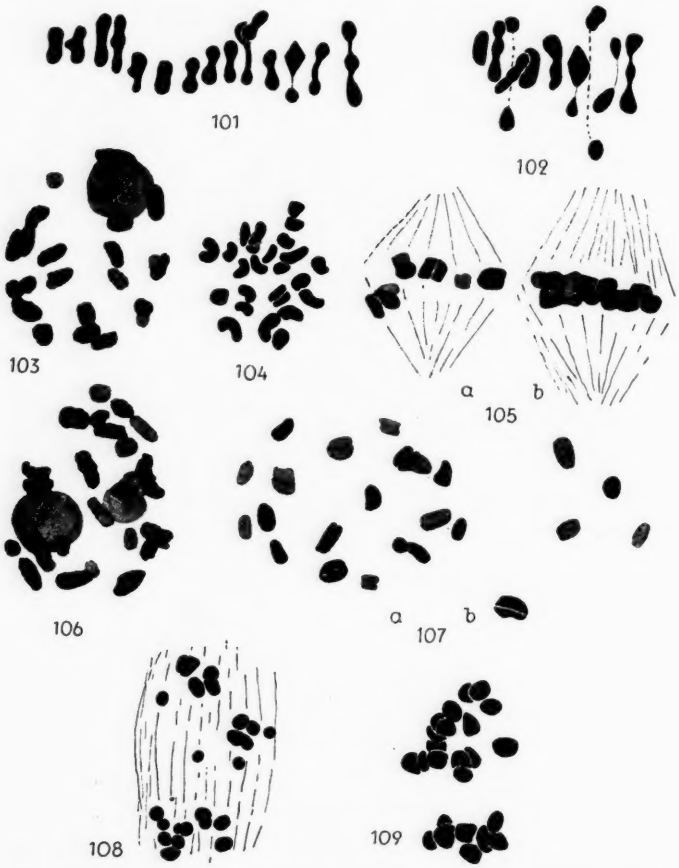
T. ceratophorum LEDEB. coll. See Figs. 97—99 and GUSTAFSSON 1935. All stages in the E.M.C:s have been observed.

T. 1930:712. See GUSTAFSSON 1935. All stages were found. Some twenty regular dyads have been recorded.

T. 1930:714. Figs. 101—102, 110—115. In the P.M.C:s this apomict shows a series of interesting phenomena which have been closely studied. As in *T. fulvum* and others no pollen is formed. Instead the P.M.C:s degenerate in the quadrinucleate stage without previously having assumed the rounded shape in most apomicts (cp. p. 10 and what was said there with regard to *Hieracium*).

Like many other tetraploids this biotype also exhibits a high rate of pairing. The figures show a number of plates (Fig. 102 an incom-

plete metaphase). Quadrivalents and also solitary trivalents have been observed. Almost complete formation of gemini is present and the



Figs. 101—109. 101—102. *T. 1930:714.* P.M.C:s 103—105. *T. alpinum* KOCH (× *Pacheri* SCH. et BIP. ?). E.M.C:s. 106—109. *T. amborum* HAGL. E.M.C:s. — 101. 1st metaphase with 1—2 trivalents and 13—14 bivalents. Note the high terminalisation. — 102. 1st metaphase (incomplete) with one trivalent and 9 bivalents. — 103. Diakinesis with 24 univalents. — 104. 2nd metaphase. — 105. Pseudohomotypic metaphase. Note the separated chromatids of one chromosome in *a*. — 106. Diakinesis with 23—24 univalents. In some chromosomes the chromatids are visible. — 107. After the dissolving of the nuclear membrane. Perhaps one association. — 108. 1st anaphase with one probable association in the middle of the spindle. — 109. 1st anaphase. — 2600—2800 ×.

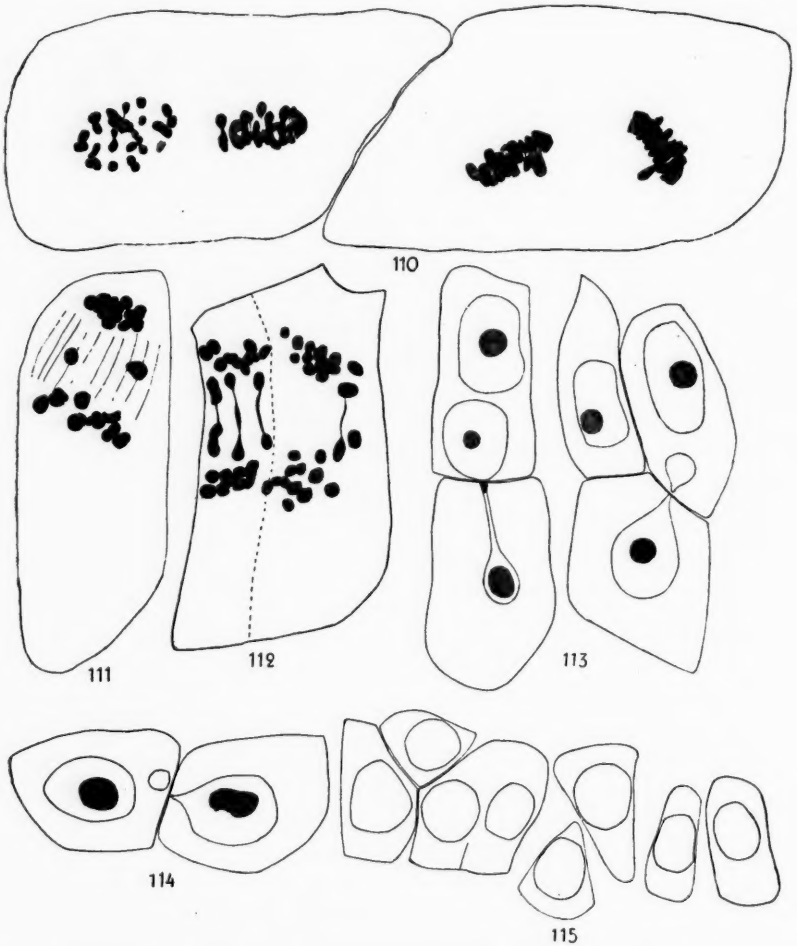
occurrence of a larger or smaller number of univalents is probably due to disturbances in the polyvalent formation. A noticeable feature is the high degree of terminalisation. Interstitial chiasmata occur and in varying frequency, but their number is proportionately rather low.

The first anomaly, which certainly conditions the second, is the frequent failure of wall-formation in the premeiotic stages so that the P.M.C:s sometimes lie in groups without any wall separating them. Fig. 110 shows four heterotypic metaphases but between them there is only one wall instead of three walls. On the extreme left is shown a metaphase seen in polar view with about 29 elements, then a metaphase seen from the side with about 11 gemini, then again another with about 13 bivalents and, finally, a metaphase with about the same number of bivalents. Fig. 112 shows a P.M.C. corresponding in size with each of those in Fig. 110. Here, however, the two plates are on the same level. The preceding premeiotic nuclear division must therefore have taken place right across instead of lengthwise. The broken line does not mark any real wall (except possibly in the lowest portion) but only a certain difference in the cytoplasm. The two plates were situated in different planes and at least as a result of fixation an evident difference appears in the viscosity of the plasm.

There is nothing remarkable in this phenomenon itself, for it has been observed in other *Taraxacum* apomicts as in many other species of plants. Correlated with this failure of wall-formation, however, is the occurrence of so-called cytomixis. By this phenomenon is meant the apparent or real movement of a nucleus and its constituent parts from one P.M.C. into another, even when there is a wall between them. In many cases there are no doubt artefacts present, in others on the other hand (according to GELIN, 1934) it is a process, the reality of which is beyond doubt. Several fixings of this biotype were made but the same result was obtained. Occasionally so-called »fragment cells» (KATTERMANN, 1933) were seen which did not contain chromatin or nuclei. Further, the spindles were often excentrically situated in the cells (Fig. 111). In addition to the ordinary plates there were also degenerating and dying chromatin masses in one corner of the cell, which in some way or other undoubtedly originated from adjacent P.M.C:s. In these cases no spindles were able to develop.

The failure of wall-formation was not the only irregularity in the premeiotic stage. The cells present were as a rule quite

different in size (Fig. 115) and were also irregular in shape. Very early stages showed proportionately a much greater number of cases



Figs. 110—115. *T. 1930:714.* P.M.C:s. — 110. Two P.M.C:s which are in reality four. Almost complete metaphases. — 111. 1st anaphase which is excentrically situated in the P.M.C. — 112. Two anaphases in the same P.M.C., also excentrically situated. — 113. Two groups of mother-cells with so-called cytomixis. — 114. Two P.M.C:s with cytomixis. — 115. A pollen loculus to show disturbed formation of cell walls. Note the diversity in size and shape. — Various magnifications, in 110—112 about 1900 ×.

without any wall than at the time of the meiosis. The walls must therefore be irregular not only as regards their position but also as regards the time of their origin. In this case one must in all probability regard the irregular wall-formation as the cause of the cytomixis. The wall-formation in »succedan» pollen-formation can also cause lagging chromosomes to be cut in two halves. A constriction of a nucleus can arise quite passively by a disturbed wall-formation in place and time, which will sooner or later bring about a severing of the two parts of the nucleus from each other. As GELIN's pictures show and as I have myself seen very often in this apomict, the constriction of the nucleus may be more or less prominent, probably subject to the varying degree of development of the wall.

Fig. 113 shows, to the left, two P.M.C:s one above the other in a stage earlier than diakinesis (the chromatin has not been drawn). The lower cell contains a strongly refractive tubular lamella which, apart from the nucleolus, contained some weak streaks of chromatin only at its extreme point but was otherwise quite clear. Fig. 113, to the right, shows three P.M.C:s, two of which lie side by side and thus have also arisen owing to disturbed membrane formation. In the upper right P.M.C. there was an isolated small nucleus discernible, containing several clumps of chromatin. This is also shown in Fig. 114. The funnel-like shape of the nucleus in the P.M.C. on the right is rather striking.

In the E.M.C:s of this apomict only dyad stages have been studied. In 12 out of 13 recorded dyads the basal cell had developed, in 1 the apical cell.

T. deliciosum HAGL. in sched. Solitary gemini have been observed in the P.M.C:s, in one case 4, in others from 1 to 3 were found.

T. Kalbfussi HAND. MAZZ. See GUSTAFSSON 1935. In the P.M.C:s as many as 8 gemini have been ascertained, solitary trivalents included. Dyads do not occur in spite of the numerous univalents. Diakineses in the E.M.C:s with unpaired chromosomes have been observed. Semi-heterotypic and pseudo-homotypic divisions, as well as interkineses and associations (4 at most) occur. 7 dyads and possibly 1 triad have been recorded.

T. alpinum (HPPE) KOCH coll. This apomict has not been studied closely. The P.M.C:s contained almost complete gemini formation. In one case 15 bivalents were observed. The formation of dyads (2,1 % of 243 tetrad stages) and of polyads (4 %) is low. This is explained

by the completeness of the formation of gemini. In E.M.C:s four dyads have been observed, three of which had the apical cell developed and one the basal one.

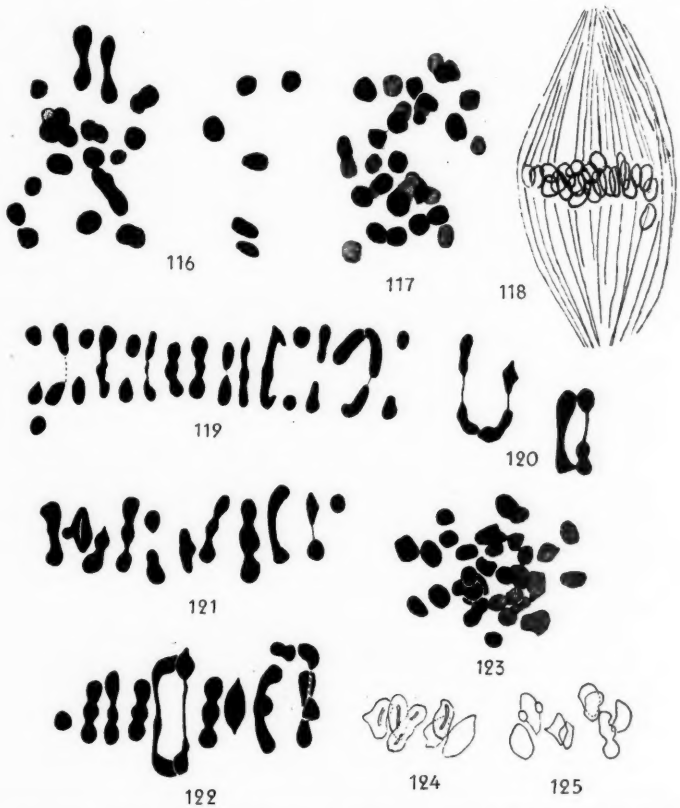
T. alpinum (HPPE) KOCH coll. (× *Pacheri* SCH. et BIP.?). Figs. 103—105. See GUSTAFSSON 1935. As a rule semi-heterotypic divisions occur, though now and then with solitary bivalents. In one case 5 such bivalents were observed. Since then E.M.C:s have been carefully studied. Diakineses with invariably unpaired elements, semi-heterotypic metaphase with or without associations (4 at most), homotypic (Fig. 104) and pseudo-homotypic (Fig. 105) divisions occur. In *a* in the last picture is shown the rare occurrence of a chromosome, the chromatids of which have commenced to separate.

T. amborum HAGL. Figs 106—109. P.M.C:s have been examined on several occasions. Divisions supplied with solitary gemini, sometimes as many as 8 in number, and frequently also semi-heterotypic metaphases have been met with. The occurrence of one trivalent is also certain. In spite of the large number of semi-heterotypic divisions and the numerous univalents when solitary gemini are present, the formation of dyads amounts to only 25 %, the proportion of polyads, on the other hand, is as high as 11,5 % (252 tetrad stages). — E.M.C:s have been closely studied. In diakineses the chromosomes are always unpaired. The metaphases show solitary associations (2 being the highest number observed). Anaphases, restitution nuclei and pseudo-homotypic divisions occur. Fig. 108 shows an anaphase, probably shortly after the stretching of the spindle. As seen, the chromosomes are distributed at random at the two poles, some remaining in the centre. Among the latter is seen a formation, which is probably an association. It is not a true geminus: it lies at right angles to the longitudinal direction of the spindle, and has probably been formed quite recently.

T. fontanum HAND. MAZZ. Figs. 116—117. The P.M.C:s show at most 8 gemini. Fig. 116 shows a pro-metaphase with 6 bivalents and 20 univalents. No trivalent has been observed. The diakineses studied in the E.M.C:s contained the zygoid number of unpaired chromosomes. In addition, one or two metaphases with a few associations have been recorded.

T. Samuelssoni DT. Figs. 126—127. The highest number of gemini in the P.M.C:s is 9, including the occasionally occurring trivalents and quadrivalents, the last-mentioned however being rare. 6 metaphases in lateral view showed respectively: 1) one trivalent, seven bivalents;

2) five bivalents; 3) one quadrivalent, seven bivalents; 4) six to seven gemini; 5) one trivalent, eight bivalents; 6) one trivalent, eight bivalents.



Figs. 116—125. 116—117. *T. fontanum* HAND. MAZZ. P.M.C. (116) and E.M.C. (117). 118. *1930:287*. E.M.C. 119—123. *T. 1930:672*. 124—125. *T. bessarabicum* HAND. MAZZ. E.M.C:s. — 116. Prometaphase with six gemini. — 117. Metaphase with at least 5 associations. — 118. Pseudo-homotypic division. — 119. Complete metaphase with one trivalent and one univalent. — 120. Two quadrivalents. — 121. Incomplete 1st metaphase. — 122. Incomplete metaphase with one quadrivalent. — 123. 1st anaphase. — 124. Incomplete 1st metaphase. — 125. Complete 1st metaphase. — 2800 ×.

Fig. 126 shows a plate with 1 trivalent (?) and 8 bivalents (?) in addition to one or two fragments, which could frequently be observed at meiosis in this apomict. Fig. 127 shows another plate with 1 trivalent (prob-

ably an interstitial chiasma in the centre) and 7 bivalents. The formation of dyads was low (5 %), the formation of polyads, on the other hand, was considerably higher (13 %, 159 cases). Hence the lagging univalents contribute less to the rise of restitution nuclei than small nuclei. E.M.C:s have not been studied.

T. porphyranthum BOISS. Only dyad stages in E.M.C:s have been studied. Of 15 such dyads 4 had the basal cell developed, but in no case was the apical cell developed.

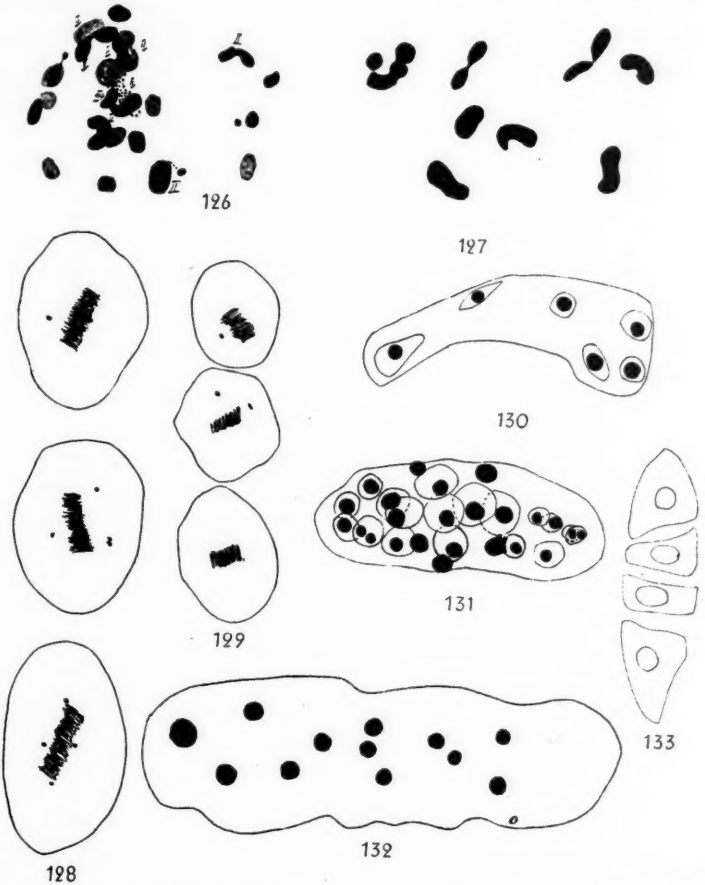
T. 1930:672. Figs 119—123, 128—132. In this apomict both P.M.C:s and E.M.C:s have been carefully examined.

Certain degenerative phenomena in P.M.C:s occur also in this biotype. Like many of the tetraploid biotypes this apomict exhibits a high degree of pairing with solitary polyvalents. Contrary to *T. fulvum* it has no pronounced terminalisation. In Fig. 119 it will be seen that of 14 bivalents at least 6 have interstitial chiasmata and in Fig. 122 with its 8 to 9 bivalents at least 5 are interstitial, in the quadrivalent one of the bivalents is also furnished with a subterminal — interstitial chiasma. As already mentioned, trivalents and quadrivalents are common. Neither are univalents rare, although the number in each plate is not large. Whether their occurrence is exclusively due to the polyvalent formation being prevented to become complete I shall not attempt to decide. In this biotype autoploidy is not so probable as in the other tetraploids.

The first abnormality in the P.M.C:s is that certain loculi contain more than the zygoid chromosome number, still the number contained did not vary, at least as far as I was able to judge. Only doubling seems to occur. Parallel with this doubling of the chromosome number there takes place an increase in the size of the P.M.C:s. — 7 cells with the doubled chromosome number gave a relative length-breadth product of 222 units, while 7 cells having the somatic number in the corresponding stage yielded a product of 123 units, that is, the product of the former was nearly twice that of the latter. The cause of this increase in the chromosome number can hardly be anything else than a premeiotic pseudo-amitosis, for no disturbances of wall-formation between the P.M.C:s has been observed.

The other degenerative phenomenon has been discerned so far only in this apomict. The tetrad stages are apparently reminiscent of those, for instance, in *T. 1930:302*, Figs. 33—34. A closer analysis, however, shows that these polyad-like formations first arise in the

tetrad stage and are nothing but fusion products of different P.M.C:s, sometimes of nearly all the P.M.C:s in a loculus. Figs. 130—132 show a couple of such cases. Their mode of origin is the same as that of the



Figs. 126—133. 126—127. *T. Samuelssonii* DT. 128—132. *T. 1930:672*. P.M.C:s. 133. *T. bessarabicum* HAND. MAZZ. E.M.C. — 126. 1st metaphase with one trivalent (?), 8 bivalents (?) and about 14 univalents. Note the fragments. — 127. Prometaphase with one trivalent and 7 bivalents. — 128. Three P.M.C:s with doubled chromosome numbers. — 129. P.M.C:s with normal numbers. — 130. Fused P.M.C:s. — 131. Fused P.M.C:s with at least 18 nuclei and more nucleoli. — 132. Many P.M.C:s (almost an entire loculus) fused. The nuclei are dissolved, only the nucleoli remain. — 133. Tetrad. — Various magnifications. Figs. 126—127 × 2600.

fusion products of peri-plasmodia and tapetal cells, but with this difference that the P.M.C:s have previously passed through a fully normal meiosis. The P.M.C:s arrange themselves close to each other, the walls are resolved so that the nuclei lie spread over the now unitary cell complex. Afterwards the nuclear membranes are resolved and only the nucleoli remain as isolated clumps in the cytoplasm. That this »degenerates», too, is evident from its abnormally great capacity of absorbing the stain.

An account has already been given of the development of the E.M.C:s (GUSTAFSSON, 1934 a). All stages have been observed. An interesting point is that the heterotypic metaphases always contained associations, although their number of course varied. This is undoubtedly due to the high degree of homology between the chromosomes. In the above paper mention was also made of the occurrence of true gemini in the diakinetic stages in both this apomict and *T. dissimile*. Thus a geminus was said to have been observed in one case in the former and *possibly* in one case in the latter. As I mentioned in the paper cited the examined diakineses of these two apomicts were rather difficult to analyse for certain and the above statement has not been verified by the conditions in other biotypes. The connections observed between the univalents may of course be artefacts, moreover a loose association may occur even in the diakinetic stage so that univalents lying loosely close to one another can give the impression of bivalents. Further analysis of diakineses in E.M.C:s have shown for certain that true gemini — if they occur — must be rare. This is also evidenced by the behaviour of the associations at metaphase and anaphase.

T. bessarabicum HAND. MAZZ. Figs. 124—125, 133. The P.M.C:s in two sexual species have been examined previously (1932 a). E.M.C:s have been studied only in this biotype. The most interesting feature is the occurrence of interstitial chiasmata and of solitary bivalents with two chiasmata each. If the associations, observed in the E.M.C:s of apomicts, may occasionally be due to primary pairing with subsequent chiasma formation, then why are interstitial chiasmata or bivalents with two chiasmata never met with?

C. ARCHIERACIUM.

The development of the E.M.C. in this sub-genus has been investigated but very little. ROSENBERG (1917) detected the so-called *Antennaria* scheme and was of opinion that the division in the E.M.C.

was purely somatic. BERGMAN (1935 a) shows that dyads are also formed occasionally. According to him the parthenogenetic division is purely somatic. He has not observed any metaphase stages. Meiosis resulting in the formation of tetrads seldom occurs, still according to BERGMAN. GUSTAFSSON (1934 b) shows the occurrence in E.M.C:s of a pseudo-homotypic metaphase in which the chromosomes are greatly contracted (circular in shape), thus in the same manner as in *Taraxacum*. The formation of dyads is shown to be a normal occurrence although not so common as a direct transition to binuclear embryo-sacs.

Owing to the material being rather small the species examined will be treated collectively.

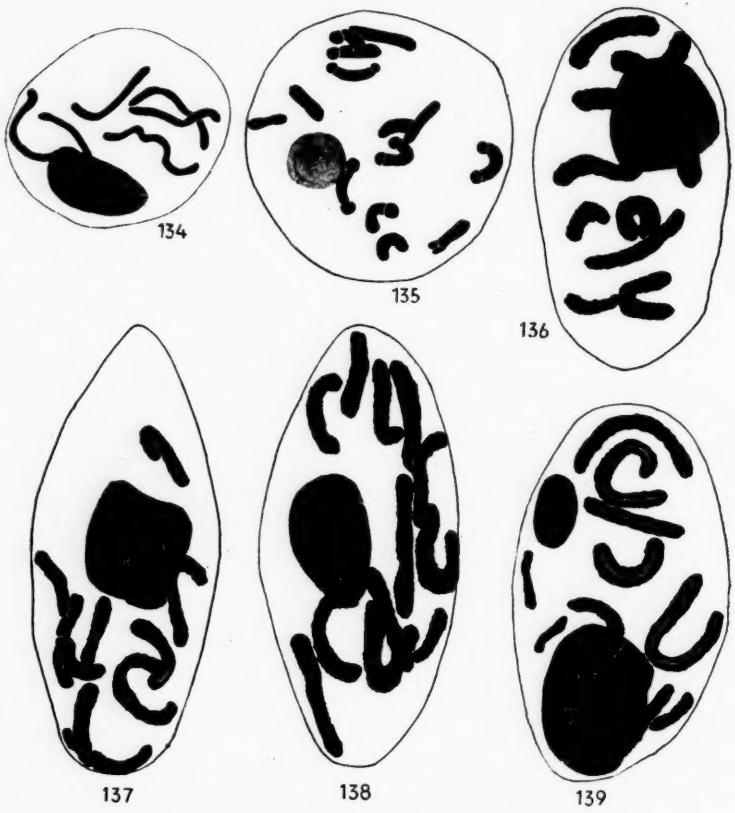
The first result that should be called attention to is the extreme rarity of the divisions. Of the tens of thousands of examined ovules only 19 were in prophase stages with differentiated chromosomes and 2 in metaphase stages, while resting stages and binuclear to multinuclear embryo-sacs were found in great numbers. *In view of the number of resting stages and embryo-sacs observed it can be postulated that the division when it has once commenced proceeds very rapidly.*

The second point that must be noted is the enormous growth of the E.M.C. and the nucleus during the resting stage (cp. BERGMAN). See also Fig. 164 *d*, which does not, however, represent the greatest growth. In general the nuclei in growing are stretched in the longitudinal direction of the cell but huge spherical stages are also met with.

The prophases do not set in equally early in the various parthenogenetic ovules. A comparison between Fig. 134 and Fig. 141 will show this. Both represent a newly begun prophase. In this way the remarkable condition arises that resting stages and embryo-sacs do not lie in any reciprocal order in the head but entirely irregularly. In the same head there are thus found widely different stages, from resting nuclei to fully developed embryo-sacs (the latter not sexual).

A third significant point is the exceedingly intense hydration of the resting nuclei so that only solitary, minute slings of chromatin occur (cp. Fig. 144, v. also BERGMAN). Such intense hydration does not occur at all in *Taraxacum* or *Erigeron* but has been observed in *Antennaria* and *Eupatorium*. Common to all three genera are the rapid accomplishment of the divisions, the late beginning of the prophases, the great growth of the cell and the nucleus and the intense hydration of the chromosomes. No other parthenogenetic genera behave in this

fashion and I therefore consider that these phenomena must signify something more than a mere coincidence. And it may be that the hydration of the chromosomes is the cause lying behind. Even if one holds the opinion that the old classification into *Antennaria*, *Taraxacum*



Figs. 134—139. E.M.C:s. Prophases with heterotypic chromosomes. 134, 136, 138—139. *Hieracium reclinatum* ALMQ. — 134. Stage immediately after the nucleus has entered the prophase. — 135. *H. triangulare* ALMQ. — 137. *H. pellucidum* LÆST. — × 2500.

and *Alchemilla* schemes should be retained, still the curious and complicated type of division in the three genera mentioned above warrants a further grouping of the *Antennaria* scheme, for example, into an *Erigeron* and *Hieracium* type.

In my opinion this abnormally intense hydration explains: 1) the duration of the resting stage during which cell and nucleus have time to grow to an unusual extent; 2) possibly the dehydration, when it has once started, increases in speed; owing to the intense hydration a long time is required for the first dehydration till the time immediately before the onset of the prophase; later on the last stage of dehydration passes so rapidly that the result will be a short prophase and a short metaphase; 3) on account of a varying intensity of hydration in the premeiotic anaphase to the summit of the resting stage, the prophase does not begin at the same time in the different ovules; the result of which will be an irregular distribution of the stages in the head and an unequal growth of the resting stages. This abnormality in hydration may bring about 4) a degeneration of certain nuclei so that on the whole they do not enter into division. For example, in *H. triangulare* about 57 % of the developed achenes did not contain any seeds. Such a high frequency of reductional divisions does not occur.

Of course the points mentioned above are in many respects hypothetical as long as we know so little about the chromosome changes in the »resting stage» between mitosis and meiosis. But the observations on which they are based are no doubt correct.

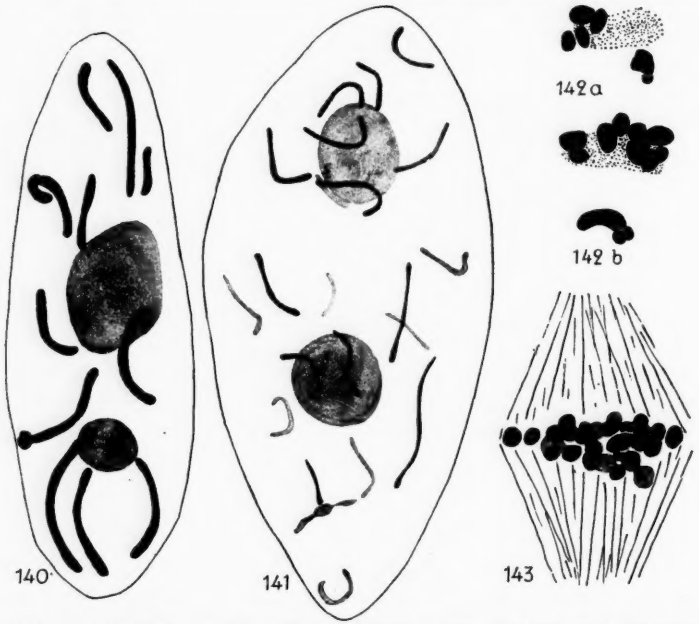
Proceeding to the appearance of the prophase it should be established once for all that the »somatic» division, which is considered to be generally met with in *Hieracium*, is only an exceptional occurrence, and *is then perhaps nothing but a degenerative product and a symptom of old age of the nucleus* (cp. p. 50). All stages reproduced originate from nuclei and cells, *which were in active growth. They cannot therefore be regarded as prophases of a normal meiosis.* In fact, this occurs seldom, as appears from BERGMAN's account. I myself have only observed a few cases of degenerating nuclei and tetrad stages. In my material they never seem to be capable of developing into embryo-sacs.

The heterotypic appearance of the chromosomes is indisputable. A variation in the contraction occurs however, compare Fig. 140 with Fig. 135. The longitudinal division was evident in several nuclei, but was only drawn in Fig. 139. In Fig. 134 the nucleus was in an early prophase stage, it had evidently just left the resting stage and the chromosomes were twisted in a zigzag fashion to a greater extent than is shown in the picture.

There is no evidence of any chromosome pairing at prophase. The chromosomes, which were quite conspicuous, were in all cases sepa-

rated from one another. Neither in the two metaphases could any traces of bivalents be discovered. Hence, in the examined prophases chiasma formation is entirely out of the question.

No restitution nuclei have been observed. The formation of dyads must therefore be due to the origin of a wall after the pseudo-homotypic division, as in *Taraxacum*. — The failure and the occurrence of



Figs. 140—143. E.M.C:s. — 140. *H. triangulare* ALMQ. Nucleus with heterotypic, but long and slender chromosomes. — 141. *H. longimanum* NORRL. Nucleus with chromosomes quite mitotic in appearance. Note the size of the nucleus. — 142. *H. longimanum* NORRL. Pseudo-homotypic metaphase with one »mitotic lagging» chromosome. Only some of the univalents drawn. — 143. *H. subampliatum* DT. Pseudo-homotypic metaphase. — 2500 ×.

wall-formation in the E.M.C:s of one and the same apomict has been described in several cases (p. 68). The dyad formation occurring now and then is therefore nothing remarkable.

The two metaphases prove conclusively that these prophase stages are not stages in ordinary meiotic divisions (a fact which is also evidenced by their occurrence in nuclei with intensive growth), for in both cases they are pseudo-homotypic metaphases, where the univalents have moved towards the centre and gathered there to be divided. Fig. 143

is undoubtedly correctly interpreted. Owing to the ovule having been cut somewhat obliquely the chromosomes do not lie in the same plane.

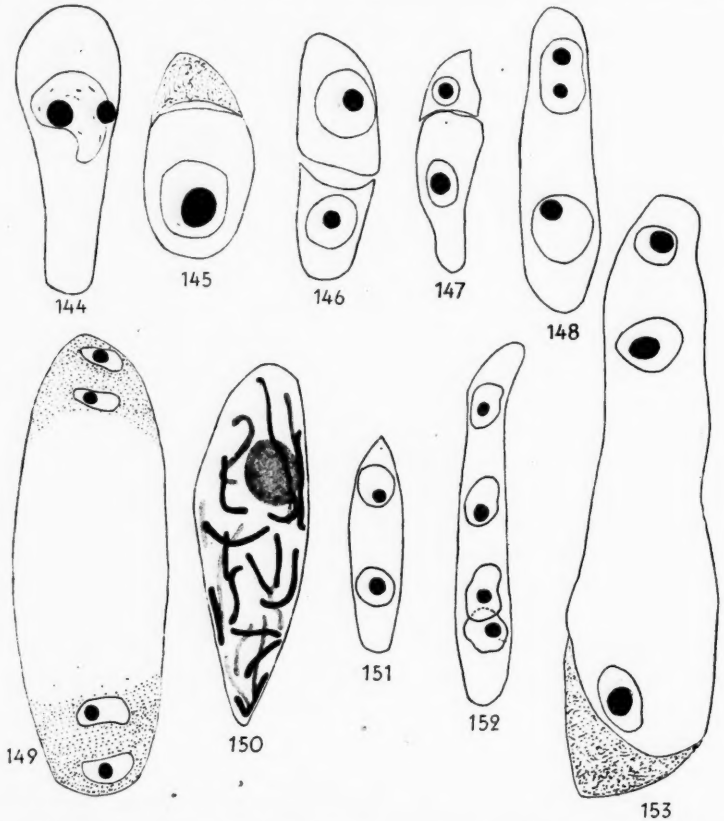
There remains Fig. 142, which on being cut was divided into two sections. In *b* is seen a chromosome lying apart from the others and presenting a somatic appearance. The longitudinal division is visible. This chromosome calls to mind what DARLINGTON has named differential precocity. That no earlier longitudinal division of just this chromosome has taken place is proved by the fact that the mitotic-like chromosome, as compared with the others, is delayed: the others have been arranged in a pseudo-homotypic plate, whereas this chromosome is still on the way. The failure of contraction is instead a primary occurrence, the chromosome has in some way or other been delayed in its contraction and associated with this is the delayed division of its spindle attachment. There is thus no evidence that this chromosome is an indication of a »somatizing» of the chromosomes with a suspended precocity.

In Fig. 140 the chromosomes are still heterotypic, although their length is considerable in proportion to their breadth. The growth of the nucleus is intense. It thus forms a transition to the nucleus shown in Fig. 141. The chromosomes here have a somatic appearance and the nucleus is the largest that has been observed in all prophases. These two conditions — as was pointed out above — are associated with one another. The ageing of the nucleus brings about a final division, the result being a somatic division as a symptom of age. It should be noted, however, that no longitudinal division of the chromosomes was visible. Of course this need not in itself involve any objection to DARLINGTON's precocity theory.

Can this picture be taken as evidence that the division in the E.M.C:s of *Hieracium* is purely somatic? Assuredly not. Because of the similarity of the chromosomes in the following metaphase (which should resemble certain metaphases in *Antennaria*) to the somatic metaphase, one is therefore not justified in calling the division somatic or regarding it as a reversion to somatic mitosis. In that case one shuts one's eyes to the prophases with heterotypic chromosomes, which are 18 times as numerous, and to the pseudo-homotypic metaphases. The so-called somatic division in *Hieracium must therefore be regarded as an exaggeration of the pseudo-homotypic type of division* and is associated with the ageing of the nucleus before division sets in.

Further, it may be mentioned here that the nuclei in the resting

stage do not only assume the spherical or fusiform shape. *Various irregular forms are not infrequently met with* (Fig. 144). It appears



Figs. 144—153. E.M.C:s and embryo-sacs. — 144. *H. longimanum* NORRL. A peculiar resting stage. — 145. *H. basifolium* ALMQ. Dyad. — 146. *H. longimanum* NORRL. Dyad. — 147. *H. lacerifolium* ALMQ. Dyad. — 148. *H. basifolium* ALMQ. Embryo-sac with two nuclei. — 149. *H. triangulare* ALMQ. Embryo-sac with four nuclei. — 150. *Erigeron annuus* PERS. Prophase with chromosomes of a mitotic appearance. — 151. Embryo-sac with two nuclei. — 152. Embryo-sac with four nuclei. — 153. *H. reclinatum* ALMQ. Dyad. — Different magnifications, in 150 2500 ×.

as if an abundant supply of fluid into the nucleus (cp. the intense hydration) causes the membrane to stretch and in this way acquire its peculiar shape. SEILER (1923) has observed a process like a passive

stretching of the nuclear membrane in *Solenobia pineti* in telophase stages when the autoregulation of the chromosome number has taken place. Perhaps the growth of the nucleus in both cases is associated with the flow of fluid.

4. THE DEVELOPMENT OF SEED IN HIERACIUM AND TARAXACUM.

Germination tests in *Hieracium* have furnished further evidence in support of the conception of the unique form of parthenogenesis, put forward and cytologically explained in the preceding pages. The

TABLE 4. *Percentage of Germination in Taraxacum Apomicts.*

Vulgaria		*Obliqua*	
T. patens DT.	96 %	*T. obliquum* DT.	94 %
T. longisquameum LINDB. fil.	76 %	*T. platyglossum* RAUNK.	
T. amblycentrum DT.?	93 %	*1930 : 44*	85 %
T. obliquilobum DT.	83 %	*1930 : 49*	90 %
T. stenoschistum DT.	90 %		
T. pectinatiforme LINDB. fil.	88 %	*Erythrosperma*	
T. fasciatum DT.	73 %	*T. lacistophyllum* DT.	91 %
T. 1930 : 3	94 %	*T. brachyglossum* DT.?	93 %
T. 1930 : 5	66 %	*T. 1930 : 26*	94 %
T. 1930 : 221	87 %	*T. 1930 : 32*	95 %
T. 1930 : 223	89 %	*T. 1930 : 40*	93 %
T. 1930 : 241	93 %	*T. 1930 : 128*	80 %
T. 1930 : 251	95 %	*T. 1930 : 167*	87 %
T. 1930 : 256	92 %	*T. 1930 : 220*	86 %
T. 1930 : 301	73 %		
T. 1930 : 315	97 %	*Spectabilia*	
		T. 1930 : 302	67 %
		T. 1930 : 304	76 %
		T. 1930 : 305	63 %
		T. 1930 : 318	81 %

With regard to the origin, etc. of the apomicts included in this investigation see GUSTAFSSON, 1932 a.

The lower percentage of germination in certain apomicts may be due to the fruits not being fully ripe when they were collected at a time (1930) when I did not know the material so well. In other cases (*T. fasciatum*) the achenes were attacked during germination by fungi. The other apomicts sent to me by HAGLUND are all characterized by a high percentage of germination. It must be mentioned here, however, that certain *Palustria* apomicts (certain *Erythrospermae*?) are perhaps characterized by an inferior germination. No conclusive examination of these biotypes has been made so far. The difference between *Taraxacum* and *Hieracium* (Table 5) is indisputable. — In all germination tests the achenes were germinated in Petri dishes between filter paper.

great difference existing between *Hieracium* and *Taraxacum* with respect to the germination and appearance of the achenes has its analogy in the different types of division in the E.M.C. Since the two successions of phenomena must be causally linked together, the different behaviour of the achenes reflects the *conditional* differences in the development of the mother-cells. Tables 4—7 give a summary of the tests made with the two genera with respect to germination.

There is not much to be said with regard to *Taraxacum*. The germination does not probably differ from that of sexual biotypes.

TABLE 5. *Germinating Capacity of Hieracium.*

	Percent. germinated	Ungerminated with contents	Percent. empty	Percent. externally useless achenes	Number of achenes
H. umbellatum L.	91	8	1		100
H. umbellatum L. (*dunense* type, achenes from 1933)	83	13	3		100
H. pellucidum LAEST.	49	27	24	4	121
H. triangulare ALMQ.	36	7	57	?	30
H. acidotum DT.	25	50	25	0	12
H. vulgatum ALMQ.					
1.	55	18	27	0	33
2.	11	42	47	11	92
H. philanthrax STENSTR.	23	48	29	7	101
H. lacerifolium ALMQ.	41	2	57	0	53
H. pannaeolum DT.	15	4	81	19	47
H. stenolepis LBG.	54	6	40	0	48
H. constringens NORRL.	7	78	15	0	116
H. lapponicum FR.					
1.	11	72	17	0	100
2.	6	81	13	?	223
H. strictum FR.	56	26	18	0	100
H. hirsutum BERNH.	36	54	10	0	99
H. pulmonarioides VILL.	65	6	29	0	94
H. subramosum LÖNNR. var. *plicatiforme* DT.	8	47	45	0	38

The *H. umbellatum* seeds were obtained from Mr. N. HAGMAN, university gardener, Lund. As the heads of these plants were for the most part unripe it was necessary to pick out only the best achenes. The last four biotypes are cultivated at Lund Botanical Gardens, while *H. lapponicum* is grown at Svalöf. The achenes of the other biotypes are from the Stockholm district and are all determined by Prof. G. SAMUELSSON. Of *H. acidotum*, *vulgatum* 1, *philanthrax*, *lacerifolium*, *stenolepis*, *constringens*, *lapponicum* 1, *strictum*, *hirsutum*, *pulmonarioides*, *plicatiforme* only the externally ripe and suitable achenes were set to germinate. Thus these seeds show too high a percentage.

There is no great delay or deterioration in the germination capacity of the achenes in the cases examined. Germination sets in and is accomplished rather quickly.

These tables form a sharp contrast to the state of things in the *Hieracium* apomicts. The two sexual biotypes of *H. umbellatum*, on

TABLE 6. *Time of Germination in Taraxacum.*

	% germination after							
	3	5	8	10	20	30	40	50days
T. patens	1	40	90	92	96	—	—	—
T. longisquameum	—	15	37	53	74	75	—	—
T. amblycentrum?	19	84	91	92	93	—	—	—
T. obliquilobum	—	48	72	73	81	83	—	—
T. stenoschistum	—	—	63	80	89	90	—	—
T. pectinatiforme	—	73	87	88	—	—	—	—
T. fasciatum	1	34	70	72	73	—	—	—
T. 1930 : 3	1	34	89	92	94	—	—	—
T. 1930 : 5	10	47	61	64	66	—	—	—
T. 1930 : 221	34	80	86	87	—	—	—	—
T. 1930 : 223	—	54	79	85	89	—	—	—
T. 1930 : 241	—	—	82	88	93	—	—	—
T. 1930 : 251	4	82	94	94	95	—	—	—
T. 1930 : 256	12	76	91	92	—	—	—	—
T. 1930 : 315	—	19	93	96	97	—	—	—
T. 1930 : 44	4	15	71	82	85	90	91	—
T. 1930 : 49	4	6	62	90	—	—	—	—
T. obliquum	—	73	94	—	—	—	—	—
T. lacistophyllum	33	91	—	—	—	—	—	—
T. brachyglossum?	—	—	—	6	89	93	—	—
T. 1930 : 26	4	63	81	92	94	—	—	—
T. 1930 : 32	—	45	95	—	—	—	—	—
T. 1930 : 40	—	45	90	93	—	—	—	—
T. 1930 : 128	—	—	35	46	70	77	80	—
T. 1930 : 167	—	5	6	58	87	—	—	—
T. 1930 : 220	31	69	77	80	86	—	—	—
T. 1930 : 302	—	—	6	12	61	67	—	—
T. 1930 : 304	—	—	—	9	22	24	73	76
T. 1930 : 305	—	1	8	18	57	60	62	63
T. 1930 : 318	—	—	—	—	12	29	57	81

the other hand, do not differ in any respect from *Taraxacum*. The inferior power of germination of *H.* »*dunense*» is due to the fact that the achenes were a year older than those of the other species.

The reduced power of germination in the *Hieracium* apomicts is worthy of attention. Even if the variation is extensive and to a certain extent is modificatorily conditioned, it is nevertheless a case of a very great reduction. This is due partly to the increased number of parthenocarpic seeds, which varies from about 10 % to more than 50 % (the

latter, for example, in *H. triangulare* and *pannaeolum*). Externally the parthenocarpic achenes are often quite indistinguishable from the normal achenes, being of the same colour and size. In every head there are, in addition to the well-developed achenes (whether normal or parthenocarpic), also a varying quantity of undeveloped achenes, which have ceased growing and are of a lighter colour. The parthenocarpy must be due to a normal formation of achenes without the

TABLE 7. *Time of Germination in Hieracium.*

	% germination after											
	3	5	8	10	20	30	40	50	60	70	80	90days
H. umbellatum 1 ...	—	37	87	91	—	—	—	—	—	—	—	—
» 2 ...	—	31	63	65	81	83	—	—	—	—	—	—
H. pellucidum	—	—	—	—	3	27	35	42	45	45	49	—
H. triangulare	—	—	—	—	10	23	30	33	36	—	—	—
H. acidotum												
H. vulgatum 1	—	—	21	30	55	—	—	—	—	—	—	—
» 2	—	—	1	2	5	10	10	11	—	—	—	—
H. philanthrax	—	—	—	1	6	13	18	18	20	22	23	—
H. lacerifolium	—	—	—	4	25	34	40	41	—	—	—	—
H. pannaeolum	—	—	—	—	8	11	13	13	13	13	13	15
H. stenolepis	—	—	10	17	50	52	54	—	—	—	—	—
H. constringens	—	—	1	3	3	4	4	4	4	6	6	7
H. lapponicum 1 ...	—	—	—	2	7	8	9	10	10	11	—	—
» 2 ...	—	—	—	2	4	5	6	6	6	6	6,3	—
H. strictum	—	—	5	11	45	56	—	—	—	—	—	—
H. hirsutum.....	—	20	32	36	—	—	—	—	—	—	—	—
H. pulmonarioides	—	38	63	64	65	—	—	—	—	—	—	—
H. subramosum var. *plicatiforme*	—	—	—	—	3	6	8	—	—	—	—	—

corresponding production of seeds. *Hence the former process is independent of the latter.*

As column 2 in Table 5 shows, parthenocarpy cannot alone explain the failure of germination. The number of ungerminated achenes, which contains seeds, varies from 2 % to 80 %. This is not due to the immaturity of the head, for the achenes were collected from fully developed heads. Further, these achenes cannot be distinguished externally from the normally germinating ones. The explanation is therefore that the seeds have not reached that stage of development at which they are capable of penetrating the ripe pericarp, or they are incapable of developing at all. An examination of the non-germinating, but full achenes of *H. lapponicum* and *H. constringens* shows that although the

achenes are of the same size, the seeds are variable in size and consequently the formation of the embryos must have started at different times in different flowers.

This is confirmed by the non-germinated achenes, from which the pericarp has been removed after some time. In *H. vulgatum* the pericarps were removed from 9 ungerminated achenes after 32 days. Six of them were set for continued germination, in 4 of these radicles and cotyledons had developed after 8 days. The same procedure was performed in *H. lapponicum*, the first time after 35 days' failure to germination, the second time after 48 days. Of the 15 embryos on the first occasion 7 had developed within 18 days. On the second occasion 20 embryos were prepared, 10 of which were kept in continual darkness. Of the latter 1 germinated in 6 days. Of the 10 remaining embryos 2 germinated in 3 days, 1 in 4, 5, 9, 10 and 18 days respectively. In *H. hirsutum* the pericarps of the ungerminated achenes were broken after 40 days in order to ascertain the percentage of empty fruits. In this process the radicles were of course injured in many cases whereas the cotyledons were undamaged. In practically all the embryos the cotyledons had commenced to become green after 5 days. These results prove that the seeds must attain a certain size in order to be able to develop or to break the pericarps. If the pericarp is removed a great percentage of the seeds are capable of getting green. *H. constringens*, which shows an unusually low percentage of germination, had achenes in which the embryos were frequently very small and transitions were found from empty achenes to normal seeds.

Attention must also be called to the uneven rate of germination. See Table 7. While germination in the *Taraxacum* apomicts and the sexual *Hieracium umbellatum* takes place rather quickly, in the *Hieracium* apomicts the beginning and the end of germination are delayed. In some biotypes the achenes still continue germinating after a period of 3 months. In only a few of them is the germination curve furnished with a maximum point, in the majority of cases the achenes germinate one at a time quite independently of each other. This confirms the results mentioned above. *The embryos have evidently reached an unequal stage of maturity, when the pericarp is completed, and therefore germinate irregularly.* Some of them, it is true, have not developed so far as to be able at once to break through the pericarp, but after certain divisions and absorption of water they finally ripen. Other embryos (which probably comprise the great majority in several apomicts) have

not developed so far by the time the achene has become ripe that they are capable of growing at all, and therefore die sooner or later.

All these facts obtain their natural interpretation when viewed in the light of the unique form of parthenogenesis occurring in *Hieracium*. A division occurring at a different time in different ovules was cytologically revealed, whereby flowers of the same age contained stages from resting nuclei to multinucleate embryo-sacs. A result of the different earliness of the divisions will be the unequal age of the embryos in the ovules. If the achene wall develops independently of the development of seeds then achenes with embryos of different ages must arise, which are consequently unequal in size and possess unequal capacity to germinate. The high percentage of empty achenes also shows that the embryo has either not been formed at all or has at any rate not reached beyond the microscopic stage. Perhaps it is also associated with a degeneration of resting nuclei in the E.M.C:s.

Since the »somatic type of division» is formed last, then the embryos which arise through this division will never or seldom reach such an advanced stage of development that they will be able to germinate. Thus this division is superfluous and is of no benefit to the plant.

Finally it may also be pointed out here that my cytological material of *Hieracia Rigida,* to which *H. lapponicum* belongs, has never contained a single prophase in which the chromosomes were differentiated, on the other hand both resting stages and embryo-sacs have been met with. The divisions probably take place very rapidly. Of the *Hieracium* apomicts examined, *H. lapponicum*, together with *H. constringens*, has the lowest percentage of germinative achenes. The great majority of the achenes, although they are only about 10 % empty, lack the power of developing. *Rigida* comprise a group of apomicts which are closely related to *H. umbellatum* and thus also to the apomict examined by BERGMAN, which, according to him, had »a purely somatic division». Poor germination and this type of division are associated with one another. In biotypes with an increased frequency of »somatic metaphases» the percentage of germination must be decreased and vice versa. This is perhaps the reason why the conditions, as described above in more suitable material, could not be shown in BERGMAN's *Hieracium umbellatum* forma apomicta.

KIELLANDER (1935) has shown parthenogenesis of the »*Hieracium-type*» to occur in *Poa serotina.* He has found all the cytological characters mentioned above. One metaphase in the E.M.C. has been seen

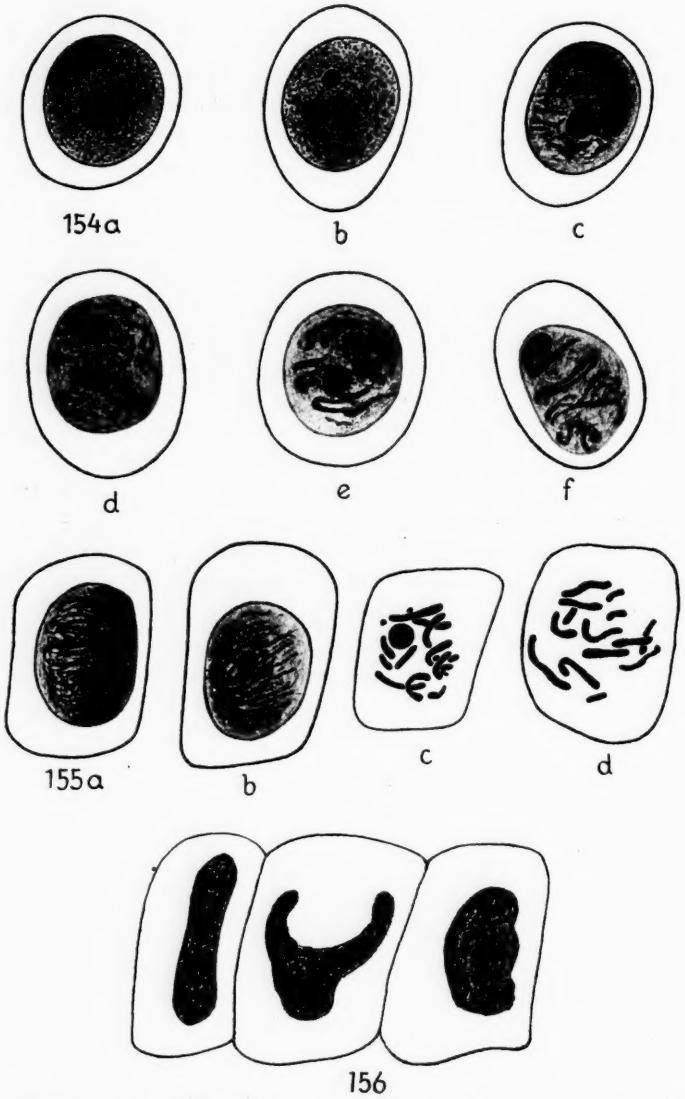
possessing chromosomes with a vegetative appearance. He has not examined the germination of the seeds. Dr. SYLVÉN, Svalöf, has told me, however, that it is a well-known fact that *Poa serotina* always gives a percentage of very bad yield of seeds, lower than in any other examined *Poa* species. *Not only a lower germination power of the developed fruits, but also an abortive and rudimentary formation of embryos occurs to a large extent.*

5. THE MALE DIVISION IN H. LAPPONICUM.

Meiosis in *Archieracium* proceeds along two roads: 1) the *H. boreale* type, the metaphase chromosomes are contracted, a varying number of gemini is formed, the border-line case being the semi-heterotypic division without any pairing (the *H. laevigatum* type); 2) the *H. pseudoillyricum* type, the nucleus undergoes a contraction stage instead of the semi-heterotypic prophase, in the following »diakinesis» (interkinesis) the chromosomes appear divided lengthways and at metaphase have the usual homotypic (»somatic») appearance.

As ROSENBERG himself points out (1927, p. 330) the enhanced mitotising is no indication that meiosis has been omitted, instead it is only a sign that the homotypic division has interfered with the heterotypic division, in place of which a contraction stage sets in. There is no »lack of precocity» present. The difficulty of reaching a somatic division in the sexual organs is all the more remarkable as such a division, according to the precocity theory, should be accomplished very easily.

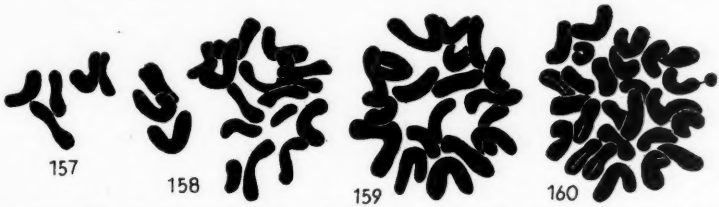
A third type of division, to which ROSENBERG does not attach any importance, is represented by *H. pulmonarioides* (1927, Fig. 4) and *H. intybaceum* (Fig. 6). In spite of an omitted chromosome contraction (DARLINGTON: change of precocity) the semi-heterotypic metaphase takes place, followed by the anaphase (the stretching of the spindle: Fig. 4 *A*—*B*) whereby the univalents are irregularly distributed to the two poles. No equational division in the first division occurs. No earlier division of the chromosomes and the spindle attachments resulting in the omission of contraction has occurred, nor is it noticeable. This peculiar phenomenon *need* not, however, be incompatible with DARLINGTON's theory if we »only» postulate a change in the nature of the spindle so that its stretching takes place at an earlier stage than in the usual semi-heterotypic metaphases, before the contraction has reached its climax. Judging from the figures, however,



Figs. 154—156. *T. lapponicum* Fr. P.M.C:s. In place of meiosis a somatic mitosis occurs, which runs regularly till metaphase. After that stage (the anaphase movement inhibited) the nuclei degenerate. — 154. P.M.C:s from the same loculus. The resting stage in 154 *a* and *b* is changed into a prophase with mitotic chromo-

this is not very probable, nuclear membrane and nucleolus are resolved and yet the chromosomes are still »somatic».

H. lapponicum Fr. (Figs. 154—160, 167), an apomict belonging to the group *Rigida*, shows a purely somatic division. After resting stages without the intense hydration that characterizes the E.M.C:s, prophases are formed exactly similar to those of mitosis. At first the chromosomes have the spireme-like appearance well-known from that stage, in length they considerably exceed the prophase chromosomes in the E.M.C:s. During the course of prophase they are contracted, it is true, but not more than in the division of the root-tips. There is some variation in the contraction at the beginning of metaphase, a thing which also occurs in vegetative organs but is more



Figs. 157—160. *T. lapponicum* Fr. P.M.C:s. — 157—159. Three incomplete metaphases from adjacent cells. — 160. Metaphase with 27 chromosomes. One satellite visible. — 2500 ×.

noticeable in the P.M.C:s owing to the number of divisions. Satellites were occasionally visible (Fig. 160).

There can hardly be any doubt as to the true mitotic nature of the divisions. Figures and microphotographs demonstrate this. It is therefore all the more remarkable that not even this division has become regular. The chromosomes remain lying in the metaphase position and are hydrated after a longer or shorter period of time, irregular nuclear membranes arise round them (Figs. 156, 167) and these nuclei degenerate. In spite of the purely somatic pre-stages physiological conditions prevent the divisions from ever being accomplished. *Hence even this proves that the physiology of the sexual organs counteract the formation of mitotic divisions instead of meiotic.*

somes in 154 *c*—*f*. In reality the P.M.C:s are not so round in shape as these figures show. — 155. Another series. The early prophases in 155 *a*—*b* resemble the so-called spireme stage in normal mitosis. *c* shows a late prophase, but *d* an early metaphase. — 156. Three adjacent cells, after the metaphase stage with the chromosomes again hydrated. The formation of a new nuclear membrane around them. After this stage the chromosomes become more hydrated and the nuclei degenerate. — Drawn by P. A. Olsson. — 1500 ×.

DARLINGTON's precocity theory can hardly be quite correct in its present formulation.

This theory requires, besides, a prolongation of the resting stage. But nothing of that kind occurs. Nuclei and cells do not grow beyond the normal stage in the P.M.C:s, which is in sharp contrast to the state of things in the E.M.C:s. Instead the angular, not round, cells lie close to each other, in the same manner as found by ROSENBERG and BERGMAN in other apomicts.

Pollen is rarely formed and is of poor quality. As it cannot be produced in the manner described above another type of division must also be accomplished. Solitary P.M.C:s — with larger nuclei — occur. Owing to their rarity it has not been possible to study them closely. As in the E.M.C:s the chromosomes are shorter and thicker at these prophases. After these stages it is probable that semi-heterotypic metaphases (which are common in *Rigida*) are formed, and subsequently solitary dyads and tetrads.

Finally, it may be pointed out here that no agreement has been ascertained between the types of division in the P.M.C:s and the E.M.C:s in *Archieracium*. As in *Taraxacum*, they are independent of one another.

6. ERIGERON.

Investigations concerning this genus have been published by HOLMGREN (1919), TAHARA (1921), CARANO (1922), and MC DONALD (1927). See also SÖDERBERG, 1929. Three species, *E. annuus*, *E. ramosus* and *E. mucronatus*, have been shown to be parthenogenetic. All three belong to the *Antennaria* scheme. No change of precocity takes place. Only exceptionally did HOLMGREN find diakineses with chromosomes having a mitotic appearance in *E. ramosus*, and he considered them to represent early stages (1919, p. 26). Instead the diakinetic stages exhibited the zygoid number of contracted chromosomes, which at metaphase lay spread along the spindle. With regard to the following stage he says (p. 25): »Durch das Studium einer grossen Anzahl dieser Entwicklungsstadien liess es sich aber feststellen, dass die Bilder von dem Aussehen der Fig. 5 *d* nur die langsame Einordnung der Chromosomen in die Äquatorialplatte, wo sie sich früher oder später alle befinden, verraten». — (Fig. 5 *d* is a metaphase with scattered chromosomes.) — Thus it corresponds to the division I have called pseudohomotypic.

TAHARA (1921) furnishes evidence of the same thing. Another

very interesting feature is his analysis of the failure of chromosome pairing at diakinesis and metaphase. His Figs. 9—13, Pl. IV show the progressive change in the nucleus, and on pages 30—31 he says: »Der Kern geht inzwischen zum Vorbereitungsstadium für die Reduktionsteilung über. Die feineren Kernfäden reihen sich deutlich an einander, wie bei den Pollenmutterzellkernen. — Die homologen Kernfädenschenkel kommen für immer nicht zur engeren Berührung. — Erst im späteren Diakinesenstadium (in my opinion in the pre-diakinetic stage) tritt ein die Parthenogenesis hindeutendes Anzeichen deutlich zum Vorschein. Die bis dahin zu Gemini gepaarten Chromosomen entfernen sich aus einander und verteilen sich gleichmässig an die Kernwandung». — Undoubtedly zygotene pairing occurs here, although chiasma formation, which leads to the origin of true bivalents, fails for some reason or other.

My studies of *E. annuus* and *ramosus* have not been extensive. The main purpose was only to find out the nature of the division in the E.M.C., to see whether any change of precocity has caused »the return to somatic mitosis», whether the formation of tetrads could occur and whether any wall was formed at any time, as in *Taraxacum*.

As HOLMGREN has already observed, no retardation of the division occurs in the E.M.C:s. According to my observations it occurs instead so early that the divisions in the E.M.C:s and the P.M.C:s are almost simultaneous. Hundreds of binuclear embryo-sacs have been studied but no wall-formation has been observed between them. Neither have I seen any heterotypic anaphases or homotypic metaphases and anaphases. There is therefore no doubt that parthenogenesis in *Erigeron* is to be characterized as stabilized, in contradistinction to the case in *Antennaria*.

Fig. 150 shows the rare finding of a prophase in *E. annuus* with changed precocity, which TAHARA did not come across. A characteristic feature of this prophase is that it occurred in a head, where the divisions of the E.M.C:s were otherwise fully accomplished, although this flower was by no means at such an advanced age as in the case of *Antennaria* or *Hieracium*. In the loculi there were newly formed tetrads. There is no doubt that this prophase indicates a change in the precocity, although HOLMGREN mentions prophases with long chromosomes as an earlier phase of development than the short chromosomed diakineses (1919, p. 26).

The pictures in TAHARA's work, showing the appearance of the early prophase, are identical with those I have observed; the prophase

never assumes the appearance which is characteristic of the corresponding stage in *Hieracium*, i. e. the chromosomes are never hydrated to such an extent that they become colourless but exist as winding threads.

7. THE ZYGOID PARTHENOGENESIS IN THE CRYPTOGAMIA.

In Algae and Fungi azygoid parthenogenesis is no rare occurrence. But few, however, are the investigations that prove the occurrence of the zygoid type.

GEITLER (1927) has succeeded in showing the incidence of zygoid parthenogenesis in *Cocconeis placentula* var. *lineata*. In this variety — in contradistinction to *C. placentula* var. I — the reduction is omitted and at diakinesis 28 univalents appear instead of 14 gemini. Judging from the figures, the chromosomes have also a contracted appearance, hence no change in precocity occurs. The author mentions the occurrence of two nuclear divisions also in the parthenogenetic biotype (thus the *Alchemilla* scheme, v. p. 71).

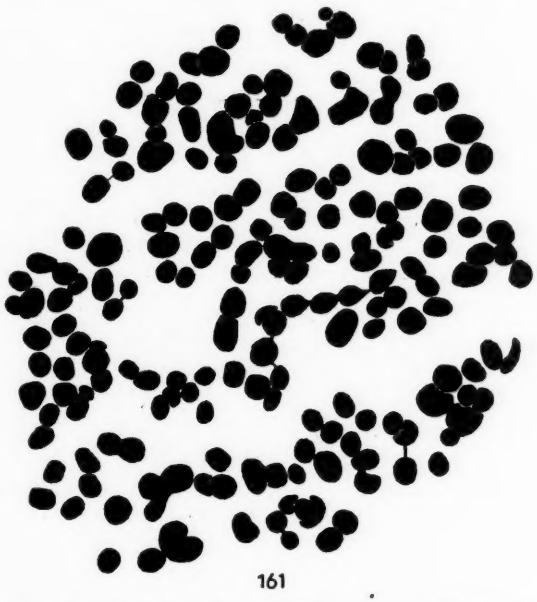
ERNST (1918) regards *Chara crinita* f. apomicta as a representative of the zygoid parthenogenesis (ooapogamy), originated by species hybridisation. WINKLER (1920) points out the possibility of the doubled chromosome number having arisen along vegetative lines. Since *Charales* consist of haploid organisms it is conceivable that azygoid parthenogenesis is present in spite of the doubled number. This question can only be solved by an examination of the nuclear division in the oospore. If the nuclear division is mitotic, then *Chara crinita* f. apomicta is an azygoid parthenogenetic species, like many haploid organisms among Fungi and Algae.

According to FARMER and DIGBY (1907) zygoid parthenogenesis is found in *Athyrium Filix-femina* var. *clarissima*. The gametophytes are formed by apospory. The sporangia are sterile, but archegonia and antheridia are produced in the normal way. The sperms are viable but no fertilisation of the egg ever occurs, for both egg and sporophyte have 84 chromosomes. An interesting feature is that the sperms enter the archegonial neck. Thus pseudogamy may be present?

A classical example of parthenogenesis in the *Pteridophyta* is exemplified by *Marsilia Drummondii*. The parthenogenetic development of the egg-cell was shown by STRASBURGER in 1907. According to him, both this biotype and allied sexual species have 32 zygoid chromosomes. In the development of the macrospores and the microspores there takes place a meiosis that is peculiar in many respects. ROSENBERG (1930, p. 23) draws a parallel between the nuclear division

in the spore mother-cells in *Marsilia* and the formation of restitution nuclei in *Hieracium*.

On account of the low chromosome number mentioned I made some fixations in the summer of 1934 of sporocarps of *Marsilia Drummondii* and its variety *tomentosa*, along with some vegetative organs of sundry species grown at Lund Botanical Garden, for the purpose of determining the exact chromosome number. *Marsilia quadrifolia*, which was reported to be a sexual form with $2n = 32$, has, however, between 100 and 140 chromosomes. Owing to poor divisions I was not successful in accurately determining the number, but the lowest is certainly $2n = 100$. In heterotypic metaphases of *Marsilia Drummondii* and its variety *tomentosa* a diploid number of about 210 was ascertained. Even here STRASBURGER gives the diploid chromosome number at 32. How such an erroneous count could have been made is inexplicable, the difference being so great. Fig. 161 shows a heterotypic metaphase in *M. Drummondii* var. *tomentosa* with at least 210 chromosomes, many of them joined into polyvalents.



161

Fig. 161. A heterotypic metaphase from *Marsilia Drummondii* var. *tomentosa* with at least 204—210 chromosomes. Polyvalents occur. — 4200 ×.

II. GENERAL PART.

1. THE MALE MEIOSIS IN TARAXACUM AND THE HYBRID HYPOTHESIS.

At about the same time ROSENBERG (1917), ERNST (1917, 1918) and WINGE (1917) advanced their theory, based on cytological facts, that apomixis is conditioned by or associated with heterozygoty and polyploidy. As SCHNARF (1929) points out ERNST never intended to maintain that hybridisation was in itself sufficient to produce apomixis. Instead he asserted only that in all carefully examined cases apomixis was associated with so many cytological and genetical disturbances that intense heterozygoty must be postulated. It is then a matter of little importance whether one assumes crossings within or without the systematic species, for the boundaries of »the systematic species» are conventional and theoretically rather arbitrary.

In fact the importance of WINKLER's criticism (1920) of »ERNST's hypothesis» does not lie so much in this sphere but rather in an examination of nomenclative questions and in a classification of zoological and botanical data. Not more than two years after WINKLER's criticism TÄCKHOLM succeeded in showing its defect, and besides that it was undoubtedly necessary to postulate crosses between distantly related biotypes as the cause of the »constant hybrid complement» within the apomictic *Rosa* groups. Although ERLANSON (1933) has in certain aspects re-examined TÄCKHOLM's results and conclusions, the main result still holds good. According to ERLANSON, the constant hybrid complement with seven gemini and 14 (21, 28) univalents represents only an ideal case, and solitary trivalents, as well as more than seven gemini, are frequently met with. Even if sexual fertilization along with heterogamy is not inconceivable in the *canina* roses (BLACKBURN and HARRISON, 1921; GUSTAFSSON, 1931; DARLINGTON, 1932, p. 372), still pseudogamy is experimentally (results unpublished) certain.

A careful analysis of meiosis in *Taraxacum* reveals the same correlation between parthenogenesis and cytological hybridity. The apomicts here must, however, be separated into two groups, one comprising all triploids and solitary tetraploids, the other embracing the remainder of the tetraploids and one hexaploid (*T. Nordstedtii*). In the former group there occurs either true alloploidy or autoploidy — the original diploid forms must then have been alloploid. Trivalents are never formed from more than 1—2 of the 8 chromosomes of the chromosome set.

If the apomicts within the genus *Rosa* (in accordance with ERLANSON's modified classification) are compared with those triploids in *Taraxacum*, which have a high rate of pairing, similarities will at once become evident. In many of them the highest number of gemini is 8 (with or without solitary trivalents) but in some, *T. praestans*, *T. melanthoides* and others, from 9 to 10 gemini are formed. Whether this implies a cross between tetraploid and diploid biotypes may be left undecided. That crosses between biotype complexes *with different chromosome numbers* may, however, have occurred is manifested by the group between the tetraploid *Spectabiliae* and the triploid *Vulgariae*, which combines features from both complexes and which was at first referred by DAHLSTEDT (1912) to the latter, but later on (1930) to the former while, according to HAGLUND (unpublished), it should form a separate group.

Several tetraploids behave like triploids, as for instance *T. Samuelssonii*, with 8—9 bivalents, of which some are solitary trivalents. Many of them, for example, *T. fulvum* and *1930:714*, show however a complete formation of gemini with a few polyvalents and univalents. Either this must imply autoploidy (the original diploid forms have then been alloploids with slight chromosome homology) or the apomicts are not at all so heterozygous that »species crossings» occur cytologically. Of course both explanations are plausible, likewise that a homologizing process has taken place secondarily. However, as the tetraploids are often closely related to the triploids (*T. laetum* and *T. obscurans*, *T. obliquum* and *T. platyglossum*) the first alternative is the more probable. *T. Nordstedtii*, in my opinion, shows the same thing. It is a hexaploid with complete pairing, solitary polyvalents and univalents but is taxonomically closely related to the triploid group between the *Spectabiliae* and the *Vulgariae* (placed there by DAHLSTEDT). Hence everything seems to indicate that it has really originated from this intermediate group by spontaneous chromosome doubling, of course not necessarily from any present existing biotype.

There remain those biotypes with varying, low or omitted pairing. Corresponding phenomena in *Hieracium* have been regarded by ROSENBERG (1917) as indicating crosses. The possibility is not excluded that they are nothing but a series of loss mutations of the superfluous pollen formation, and they are therefore no sure indication of a »species crossing». In *Hieracium* the degenerative processes in the P.M.C:s lead to a longitudinal division of the chromosomes already in the first division, but in several ways and all of them with a different

course from that of the somatic mitosis (except in *H. lapponicum*, v. p. 51). In *Taraxacum* such phenomena never occur. Here the final goal is the omitted pairing. Other phenomena, such as disturbed wall-formation, etc., arise as degenerative products.

There is also another possibility. If parthenogenesis and its most important characteristic — the failure of pairing in female prophases — must be regarded as a superstructure of meiosis, not a reversion to somatic mitosis, then the failure of pairing may have arisen simultaneously in male and female organs and is thus not due to non-existent homology. In that case complete pairing is in itself a link in a degenerative process, where genes which condition univalence in the P.M.C:s have been lost. Meiosis in *T. maculigerum* and *T. praestans*, which are closely related taxonomically but are cytologically different, can be explained in two ways; either meiosis in *T. maculigerum* is the original condition and the high degree of pairing in *T. praestans* a secondary occurrence, or *T. praestans* represents a more original condition than *T. maculigerum*. However that may be, there is a possibility that meiosis in the male organs is subject to degenerative processes.

To summarize it may thus be said that the genus *Taraxacum* furnishes another instance of parthenogenesis correlated with polyploidy and cytological hybridity. With regard to the actual method of origin of apomixis there is a great deal of evidence in support of SCHNARF's conception (1929). Sexual diploids may conceal genes that condition apomixis. By crosses these genes are brought together. The sexual maturation divisions bring about sterility, and in the absence of competing sexual embryo-sacs and embryos the tendency to apomixis can find expression.

It should be pointed out, however, that parthenogenesis in many genera probably appeared all at once and did not become stabilized by degrees. — An entirely new type of division had to be introduced in the peculiar kind of parthenogenesis occurring in *Antennaria* and *Hieracium*. It was not possible to alter directly the sexual division as in *Taraxacum* and *Erigeron*. No restitution nuclei are formed in the few sexual divisions. Instead parthenogenetic seeds are produced in a circumstantial fashion: The chromosomes are hydrated to such an extent that the result will be a long resting stage. Nucleus and cell grow abnormally. When once started the divisions proceed at a rapid rate. Occasionally the resting stages in *Hieracium* (and also in *Antennaria*) overshoot the mark, so to say, and the result will be a division

in the E.M.C:s, the metaphase stage of which resembles the somatic stage. In *Hieracium* (*Antennaria*?) the seeds formed in this manner are probably incapable of development, because the division has been retarded too long in proportion to the development of the pericarp.

2. CHROMOSOME NUMBER AND APOMIXIS.

It has always been thought that the sexual species within the apomictic genera have as a rule lower chromosome numbers than the apomicts. This is of course true to a certain extent, but Table 8 shows that this view does not embrace the whole of the facts. As far as the totally parthenogenetic genera are concerned the argument holds good on the whole, but on the other hand it does not apply to many genera of the amphi-apomictic *Rosaceae*, where a number of sexual species are known.

At the same time it will be seen that the totally parthenogenetic apomicts generally belong to classes with lower chromosome numbers than the amphi-apomicts. In *Taraxacum*, for example, the majority of apomicts are triploids, to a considerably smaller extent tetraploids and only one pentaploid and two hexaploid forms are known. In *Rubus* there occur among *Eubati veri* apomicts with 21, 28 and 35 chromosomes, and *Rubi Corylifolii*, which are crosses between *Eubati veri* and the tetraploid *R. caesius*, have (21), 28, 35, 42, 49 and 56 chromosomes. The difference is due to the fact that the crossing processes are continually going on in the amphi-apomicts and that the apomictic mode of propagation thus gradually increases in intensity until embryo-sacs no longer function or develop. In the total apomicts within *Taraxacum* and *Archieracium*, etc., parthenogenesis has evidently arisen all at once (as already pointed out by ERNST in 1918), and no segregation products with increased chromosome numbers have subsequently been formed.

No doubt the discovery of exclusively diploid sexual species in many genera is due to the fact that the sexual species are few in number as compared with the apomicts and this in turn is due to their having to a certain extent the character of relics (at least this is the case in *Taraxacum*), of which it is moreover often difficult to obtain material for examination. In genera with a relatively large number of sexual forms these also occur in the higher classes, in *Erigeron* the species with the highest number of chromosomes are indeed sexual.

Another important point for the correct interpretation of apomixis may be gathered from the same table and the above discussion.

TABLE 8. *The Chromosome Numbers in the Apomictic Genera.*

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16 × basic number
Rosa															
Sexual	×		×		×										
Apomictic			×	×	×										
Rubus															
Sexual	×		×		×		×		×		×				
Apomictic		×	×	×	×	×	×								
Potentilla															
Sexual	×		×		×		×		×		×		×		×[1]
Apomictic	×			×	×	×	×				×				
Sorbus															
Sexual	×		×												
Apomictic		×	×												
Pilosella															
Sexual	×														
Apomictic			×	×											
Alchemilla															
Sexual															
Apomictic						×		×		×		×		×	
Antennaria															
Sexual	×	×													
Apomictic		×	×		×										
Taraxacum															
Sexual	×														
Apomictic		×	×	×	×										
Archieracium															
Sexual	×														
Apomictic		×	×												
Chondrilla															
Sexual	×														
Apomictic		×	×												
Erigeron															
Sexual	×	(×?)	×		×										
Apomictic		×													
Eupatorium															
Sexual	×														
Apomictic		×													

[1] The possibility is not quite excluded that these forms of *Potentilla* with high chromosome numbers are pseudogamous. They are concentrated, however, to the groups *Graciles* and *Haematochroae* and not to the groups examined by MÜNTZING (1928, 1931) and shown by him to be pseudogamous. SHIMOTOMAI (1930) states that the group *Haematochroae* especially consists of garden forms. Their sexual nature is therefore probable.

Apomixis cannot be caused by hybridisation and increase in the chromosome number alone. A few years ago (1930) I called attention to the fact that the North American *Rubi Eubati*, although many of them are closely related to the European blackberries and like the latter hybridize intensely and possess high chromosome numbers, have nevertheless remained sexual. Thus apomixis must be a »Begleiterscheinung» and not a »Folgeerscheinung» of the hybridisation. Apomixis is a phenomenon, the origin of which is aided by the two processes mentioned above but is not determined by them. The only way in which the origin of apomixis can be explained is that it is caused by specific genes. Hybridisation and increase in chromosome number proves that the genes are often of a complementary nature and that apomixis is therefore a phenomenon determined by several genes. Nor is the possibility excluded that apomixis is conditioned by purely recessive factors. Certain facts relating to the genus *Poa* are considered by MÜNTZING (1933) to argue in favour of this view. In 1930 I myself considered that in *Rubi Eubati*, judging from LIDFORSS's results, pseudogamy is conditioned by a series of recessive factors.

3. THE AUTOMICTIC PARTHENOGENESIS AMONG ANIMALS.

The zygoid parthenogenesis found in animals has been divided by ANKEL (1929, p. 341) into three groups: 1) The chromosome conjugation fails. The usual occurrence in both plants and animals. 2) At first chromosome conjugation occurs but is not accomplished. According to my interpretation this conjugation means probably zygotene pairing. *Daphnia pulex* and *Polyphemus pediculus* belong to this group, »die seinerzeit der Chromosomentheorie zu schaffen machten, weil hier kein Zusammenhang zwischen Konjugation und Pseudoreduktion nachzuweisen war: Trotz des Auftretens von Konjugationsbildern erscheint in der einzigen Reifungsteilung die diploide Zahl». 3) Bivalents arise and the first division leads to a reduction in number. *Rhabditis monohystera* and *Solenobia pineti* belong to this group. ANKEL places *Aphis palmae*, too, on the same level with them. The last-mentioned, however, has probably no chiasma formation but only zygotene pairing (p. 78) or — according to DARLINGTON — association due to terminal affinity; it should thus belong to the second group.

Of these Group 3 forms a transition to what ANKEL calls automictic parthenogenesis. As was pointed out by PRELL already in 1923 the conception of parthenogenesis in animals is historically determined. In

this way both apomictic phenomena (»true parthenogenesis») and amphimictic phenomena (»false parthenogenesis») are grouped together under this conception. By amphimictic parthenogenesis PRELL means (p. 204), »wenn ein Ei zwar nicht durch eine männliche Geschlechtszelle befruchtet wird, wenn aber auf irgend eine andere Weise die azygoide Chromosomengarnitur auf den zygoiden Zustand gebracht wird».

According to PRELL and the view advanced here, the essential feature of zygoid parthenogenesis is that a reduction caused by zygotene pairing with a subsequent chiasma formation is omitted in the first division. PRELL, like SEILER (1923) and HARTMANN (1933), but contrary to ANKEL (1929), thus correctly refers *Solenobia pineti* to false parthenogenesis.

In *Rhabditis monohystera* BELAR (1923) found synaptic contraction, bivalent formation and a reduction in the chromosome number (p. 515). At telophase the chromosome number is then regulated by a splitting of the chromosomes, which is to be regarded as the second, here suppressed, maturation division. In *Solenobia pineti*, as in *S. triquetrella* and the bisexual species, there occur synaptic contraction, diplotene stages and reduction in number. The second maturation division »wird anscheinend wohl vorbereitet, nicht aber ganz durchgeführt, es werden nur die Chromosomen durch Längsteilung halbiert, zur Ausbildung einer Spindel kommt es nicht» (SEILER, 1923, p. 62).

There is not such a great contrast between regulations occurring before and after the first cleavage division in case of a reduction of the chromosome number that these two phenomena should be grouped separately. The point of importance is whether chiasma formation (crossing-over) takes place or not, and, in my opinion, this alone should be employed as the basis of classification. From this point of view both *Rhabditis monohystera* and *Solenobia pineti* should be referred to the pseudo-parthenogenetic group. At any rate we are not justified, as ANKEL has done (1929, p. 354), in drawing conclusions from these isolated findings that automictic parthenogenesis is a forerunner of zygoid parthenogenesis.

Is then the so-called automictic parthenogenesis an apomictic phenomenon? According to WINKLER's definition it is certainly not. ANKEL asserts that the nuclear fusion taking place has the character of a fertilization. Even if the two nuclei are genotypically identical there is a »tension» between them: in *Solenobia triquetrella* both

cleavage nuclei have a conjugating tendency, and in *Lecanium hesperidum* the polar nucleus follows the egg nucleus deep down into the egg plasm. — This proves the correctness of PRELL's designation, false or amphimictic parthenogenesis.

In conclusion it may be pointed out here that automictic phenomena occur perhaps also among the higher plants (*Allium odorum* and others). ROSENBERG (1930, p. 54) also calls attention to one of CARANO's pictures (1922), which possibly shows the formation of a restitution nucleus in the homotypic division.

4. WALL-FORMATION AS A PRINCIPLE OF CLASSIFICATION IN THE PARTHENOGENETIC PHANEROGAMS.

Four and two daughter nuclei respectively are thought to arise from the E.M.C., according to the *Alchemilla* and the *Taraxacum* schemes, whereas in the *Antennaria* scheme the E.M.C. give rise direct to the embryo-sac. So they have been deemed to mirror a *gradual recession* from the sexual condition. This opinion, which is maintained by STRASBURGER and others, will not be specially dealt with here. Bound up with this question, however, is the much more important question as to the correctness of drawing a parallel between the three schemes and the Normal, *Scilla* and *Lilium* types occurring in sexual species (v. inter alia ROSENBERG, 1930, and GUSTAFSSON, 1935), which are characterized by the same wall-formation. It is of course important to ascertain whether the basis of classification employed is built on accidental occurrences or on genetically definite causes. If it is proved that the three schemes correspond to systematic groups, in which the sexual species have parallel types of development, it will at once be evident that they are justifiable in their present form. That this is not the case is shown by the following tabulation, based on SCHNARF's work (1931). Those cases of parthenogenesis, which he considers uncertain, have not been included.

Elatostema: The Normal type in sexual species. *E. sessile* has the *Antennaria* scheme, *E. acuminatum*, besides azygoid also zygoid embryo-sacs. In the last-mentioned case mostly the *Antennaria* scheme is present but formation of wall can occur so that the *Taraxacum* (?) and the *Alchemilla* schemes arise.

Houttuynia: Normal type in the sexual species, the *Scilla* type also occurs in the closely related genera *Saururus* and *Anemiopsis*. *H. cordata* is said to have the *Alchemilla* scheme. See further p. 72.

Helosis: According to SCHNARF, sexual species within the family *Balanophoraceae* follow the *Lilium* type. *H. guyanensis* has mostly the *Antennaria* scheme, although the *Taraxacum* scheme occurs occasionally.

Balanophora: Concerning the sexual species see above. *B. elongata* and *B. globosa* have, according to ERNST, 1914, E.M.C:s which in more than 50 % of all cases divide into two daughter cells. Thus both the *Antennaria* and the *Taraxacum* schemes occur here. According to KUWADA (1928), *B. japonica* has the *Taraxacum* scheme exclusively.

Alchemilla: Normal type in the few sexual (?) species examined, the *Alchemilla* scheme in the apomicts. See further p. 69.

Wikstroemia: The sexual forms belong to the Normal type. *W. indica* has always the *Taraxacum* scheme. STRASBURGER says however (1909, p. 69): »Eine feste Scheidewand wird zwischen den beiden Zellen nicht ausgebildet, sie erscheinen vielmehr nur durch einen hellen Zwischenraum von einander getrennt, so dass leicht bei geneigter Lage dieser Trennungsfläche die Vorstellung eines einzigen zweikernigen Protoplasten hervorgerufen kann». According to STRASBURGER, in exceptional cases several nuclei can also arise, between which a cell membrane is formed.

Salomonia (*Epirrhizanthes*): The sexual forms have the Normal type. *S. cylindrica*, according to SHADOWSKY 1911, has the *Alchemilla* scheme. See further p. 72.

Cotylanthera: The sexual species belong to the Normal type. *C. tenuis* has, according to OEHLER, the *Alchemilla* scheme. See p. 71.

Chondrilla: Sexual species have the Normal type. Apomicts belong to the *Taraxacum* scheme. Regarding PODDUBNAJA-ARNOLDI's information about the *Alchemilla* scheme see p. 71.

Taraxacum: Always Normal type in sexual species. Apomicts belong to the *Taraxacum* scheme; very seldom to the *Antennaria* scheme (?).

Erigeron: Most sexual species follow the *Scilla* type, but the Normal and the *Peperomia* types also occur. According to SCHNARF, the *Lilium* type is also met with. Apomicts belong to the *Antennaria* scheme.

Eupatorium: Sexual forms belong to the Normal type, apomicts to the *Antennaria* scheme.

Hieracium: Sexual forms belong to the normal type, apomicts to the *Antennaria* scheme but also, and differently in different form-circles, to the *Taraxacum* scheme.

Antennaria: Normal type in the sexual species, the *Antennaria* scheme in the apomicts.

Artemisia: The Normal type in the sexual species. *A. nitida* has, according to CHIARUGI, the *Antennaria*, *Taraxacum* and *Alchemilla* schemes.

Burmannia: Closely related sexual forms have the Normal or *Scilla* type. *B. coelestis* mostly follows the *Antennaria* scheme but frequently and in varying numbers in different flowers also the *Taraxacum* scheme.

Thismia: Sexual species have the Normal type. *T. javanica* has been reported to have the *Alchemilla* scheme. See further p. 72.

As will be seen from the above classification there is no correlation between the *Lilium*, *Scilla* and Normal types, on the one hand, and the *Antennaria*, *Taraxacum* and *Alchemilla* schemes, on the other. An illustrative example of this is the genus *Erigeron*, in which the sexual species manifest quite different types of development, the dominating one being the *Scilla* type. In spite of this the *Taraxacum* scheme

is not the most commonly occurring one, the *Antennaria* scheme being the only one discovered so far.

Since this parallelism does not occur it is important for a correct classification to ascertain whether there is such a parallelism between the formation of a wall and the method of division in the E.M.C:s. As far as can be judged, the »somatic division arising through altered precocity» does not result in the formation of any wall. After the pseudo-homotypic division wall-formation can occur or fail, the former in *Taraxacum* and *Chondrilla*, the latter in *Erigeron*. Restitution nuclei chiefly result in the formation of dyads. In *Erigeron mucronatus*, in which undoubtedly — as pointed out by ROSENBERG in 1930 — restitution nuclei can arise, no wall is ever formed, according to CARANO. An important proof of the want of agreement between nuclear division and wall-formation has been supplied by OKABE (1932). At the heterotypic metaphase in *Ixeris dentata* there are 21 chromosomes (always unpaired), which after the formation of a restitution nucleus give rise to a normal homotypic plate containing all the chromosomes. At telophase a thin cell-plate is formed in the centre of the spindle, which however gradually disappears again.

It is known that in the *Peperomia* type — as well as in the *Scilla* and *Lilium* types — a wall is occasionally formed in the »coenomacrospore». SCHNARF (1929, p. 209) enumerates some cases in which this occurs. More frequently transitory walls, or at least cell-plates, are formed. In the third division, on the other hand, no trace of either cell-plates or wall-formation has been observed. In *Burmannia coelestis* (ERNST and BERNARD, 1912), in those cases in which no dyads occur, no walls appear, it is true, but cell-plates are plainly visible. In a number of cases these are apparently formed so strongly that the result will be a cell-division, in others the physiological conditions do not permit of the formation of a real wall. According to TAHARA, at telophase in *Erigeron annuus* a very plain cell-plate is formed, which is however gradually resolved in later stages (v. also above with regard to *Ixeris*). Although there is mostly, in those cases in which dyads arise, a physiological and morphological difference between the two cells so that already before the wall has been formed one of them is predestined to develop, there are however also other cases which show a physiological similarity. LOTSY asserts that in *Balanophora globosa* he has observed that both dyad cells can develop right up to mature endosperm and embryonal stages (cited from ERNST, 1914, p. 135). UMIKER (1920, p. 37) mentions corresponding conditions also in *Helosis*.

ERNST himself has, however, only once observed that two equal-sized, quadrinuclear embryo-sacs have developed from two dyad cells. In *Taraxacum* the macrospore determined for development, as in *Balanophora* and others, will from the beginning be considerably larger in size. In many cases it is evidently only this difference in size that decides which dyad cell will develop.

Of the genera belonging to the *Antennaria* or the *Taraxacum* scheme *Elatostema sessile*, *Erigeron*, *Eupatorium*, *Antennaria*, *Ixeris* have no wall-formation, while a wall is formed in *Wikstroemia*, *Chondrilla*, *Taraxacum* and *Balanophora japonica*. The following, *Helosis*, *Balanophora globosa* and *elongata*, *Hieracium*, *Artemisia*, *Burmannia* are both with and without formation of a wall. Thus in five cases no formation of wall occurs, in four cases a wall is always formed and in five cases both phenomena are met with. This classification thus shows the so-called exceptions to be as numerous as the two proposed types.

By means of this classification it has been shown that the division into *Antennaria*, *Taraxacum* and *Alchemilla* schemes does not correspond to or is even analogous with the division into *Lilium*, *Scilla* and Normal types for sexual plants, that the wall-formation on which the division is based does not correspond to the method of division in the E.M.C., that in many cases it is an accidental occurrence whether a wall is formed or not and that the last-mentioned cases — so far as investigations have shown — are not fewer in number than those referred to the *Taraxacum* or the *Antennaria* scheme. It may be possible to defend the retaining of this basis of division for practical reasons, but as the outstanding feature in zygoid parthenogenesis is the manner in which the zygoid chromosome number is obtained, it seems to me that too much value has been attached to it.

An interesting point in this connection is that parallel series to the three schemes are said to occur in animals. PRELL (1923) has thus divided zygoid parthenogenesis into the *Neuroterus-Antennaria* type, the *Daphnia-Taraxacum* type and the *Rhodites-Thalictrum* type. According to older data *Neuroterus* was said to lack maturation divisions entirely. THOMSEN (1927, cited from ANKEL) and ANKEL (1929) however considered this case to be doubtful. According to a number of reports even a tetrad division, with zygoid daughter nuclei, occurs in animals, a statement which ANKEL regards as doubtful. We thus see that the grouping into definite types, either in plants or animals, does not stand the test of a thorough examination.

5. THE SO-CALLED ALCHEMILLA SCHEME.

The discussion concerning the employment of wall-formation as a basis of classification for the parthenogenetic phenomena is conclusively settled by an analysis of the so-called *Alchemilla* scheme, for this must, if not excluded altogether from parthenogenesis, at least be regarded as a border-line case. The results of the investigations which have been regarded as evidence of its presence in other genera than *Alchemilla* are also rather doubtful.

If a parthenogenetic tetrad division is to be homologous with a sexual division only one division of the spindle attachments must take place. But in this way the daughter cells receive the azygoid number. To render it possible for zygoid numbers to arise either two purely somatic divisions must succeed one another or the homotypic division, in which the two plates have in some way or other obtained the diploid number, must be followed by a similar division. CHIARUGI (1926) has given a description of the divisions in the P.M.C:s of *Artemisia nitida*, whereby zygoid tetrad nuclei are said to arise. See below.

MURBECK's works (1897, 1901, 1902) are the foundation of our knowledge of *Alchemilla*. Later works by BÖÖS (1917, 1920, 1924) have in the main confirmed MURBECK's observations and have pointed out the weaknesses in STRASBURGER's opposition (1905). The character of parthenogenesis in *Alchemilla* has been discussed by TÄCKHOLM (1922), EDMAN (1929), ROSENBERG (1930), LILJEFORS (1934) and GUSTAFSSON (1934 a and b). All agree that the development of the embryo is to be regarded as aposporous. No conclusive evidence has however been obtained.

The genus *Alchemilla*, like many other *Rosaceae*, is characterized by having a multicellular archespore. Those species examined by MURBECK contained as a rule from 12 to 16 archespore cells. These cut off outwardly cover cells, and the sporogenous cells, which MURBECK and BÖÖS call E.M.C:s, begin to differentiate among themselves. The central one grows, the nucleus is enlarged in the form of a cyst and the contents pass into a synapsis-like stage. MURBECK interprets this as the beginning of a degenerative process. In his opinion the central E.M.C. does not develop any further. STRASBURGER, on the other hand, considered that he was able to show that this long synapsis-like stage was followed by a tetrad division, but without any reduction of the chromosome number. With reference to some South American species of the group *Aphanes*, BÖÖS (1917) agrees with MURBECK's point of view,

and in 1924 he showed that even *A. arvensis* is an apomict and has the same type of development. In exchange for the central E.M.C. the lateral cells divide into a number of cells and one of the latter develops further into an embryo-sac. MURBECK calls these lateral cells E.M.C:s without entering into any discussion as to the correctness of this designation, and their products he calls macrospores, although he mentions himself that the division by means of which they are produced are somatic.

By what right are these lateral cells called E.M.C:s and their products macrospores?

1) Externally the lateral cells undoubtedly resemble the axile cell. They cut off their cover cells in exactly the same manner as the axile cell, in the beginning the cells and their nuclei are of the same size, have the same plasma contents and equally large nucleoli. But while the axile cell and its nucleus at once begin to grow and enter into the synapsis-like stage, the lateral cells exhibit no tendency at all in this direction, quite contrary (as MURBECK also points out) to the occasional derivatives of the cover cells and to the so-called macrospores. *Hence, contrary to their progeny, they are not at all sexually disposed.*

2) For macrospore divisions the divisions take place unusually early, occurring at the same time as the tetrad division in the male organs. In general the division of the E.M.C. occurs in both sexual species and apomicts much later than that of the P.M.C:s. It does not take place so early even in *Erigeron annuus*.

3) The number of daughter cells produced is indefinite; according to MURBECK, three are formed mostly but also two and four occasionally, while STRASBURGER mentions as many as six.

4) These daughter cells, the so-called macrospores, frequently exhibit the above-mentioned tendencies to meiosis. In *A. arvensis* (BÖÖS, 1924) they can even form diakineses with complete formation of gemini.

5) Every one of them is physiologically capable of developing into an embryo-sac. Frequently several such embryo-sacs arise from the same triad or tetrad, although one of them will gain the ascendency later on.

6) In the *Rosaceae* there are found transitions from genera where there is no difference between axile and lateral sporogenous cells (*Rosa*), to those in which there is a physiological differentiation between these cells although they agree morphologically (*Alchemilla*), and to those where also a morphological difference exists (*Sorbus*). In the

last-mentioned case there is undoubted evidence of apospory. The last stage in this series is exemplified by *Kerria japonica* with an archespore of 2—3 cells and *Neurada* — along with several doubtful cases — with a single archespore cell. Of course this series is not represented here from a phylogenetic point of view.

As we see, it is thus rather doubtful whether *Alchemilla* belongs to the second archespore type proposed by SCHNARF (1929, p. 72), in which the archespore cell, immediately after the formation of the cover cell, becomes the E.M.C. or to the first type in which more than one somatic division is interposed between archespore cell and E.M.C. As far as I am able to judge, the lateral mother cells belong to the first type, the axile cell, on the other hand, to the second. — The main thing, however, is that *the primary and secondary daughter cells* can have the character of E.M.C:s and that the divisions by means of which they arise are not homologous with the tetrad divisions in the sexual plants.

While *Alchemilla* is undoubtedly apomictic and, apart from the discussion as to whether apospory or parthenogenesis is present, has been determined in its main features, this can by no means be said of the other genera which have been described as belonging to the *Alchemilla* scheme. These genera are *Houttuynia* (SHIBATA and MIYAKE, 1908; SÖDERBERG, 1927; OKABE, 1930), *Salomonia cylindrica* (WIRZ, 1910; REISER, 1910; SHADOWSKY, 1911), *Thalictrum purpurascens* (OVERTON, 1904; KUHN, 1928), *Cotylanthera tenuis* (ERNST, 1914, p. 132; OEHLER, 1927), *Chondrilla*, partly, (PODDUBNAJA-ARNOLDI, 1933), *Artemisia nitida*, partly, (CHIARUGI, 1926), *Thismia javanica* (ERNST and BERNARD, 1910; MEYER, 1910, 1925), *Marsilia Drummondii* (STRASBURGER, 1907).

Of these *Thalictrum*, *Chondrilla* and *Marsilia* can be excluded at once. As the chromosome number in *Marsilia* is probably seven times greater than STRASBURGER reported no conclusion whatever can of course be drawn from his data concerning zygoid tetrad cells. KUHN has shown that *Thalictrum purpurascens* is a sexual species. PODDUBNAJA-ARNOLDI's data of the *Alchemilla* scheme in *Chondrilla* are based only on the fact that tetrads, triads, etc., are frequently formed. If the chromosome number is diploid the development takes place, she says, in accordance with the *Alchemilla* scheme, on the other hand, if the number is haploid the Normal type is followed. — There is no reason for assuming any form of development than the latter, zygoid tetrad nuclei have not been observed.

Recently *Cotylanthera* has been described as parthenogenetic by OEHLER. His pictures however show — in my opinion — that the development does not at any rate take place according to the *Alchemilla* scheme.

After synapsis in the male organs there follows a diakinesis in which a number of chromosomes lie scattered in pairs all over the nucleus. According to OEHLER,

these chromosomes do not consist of gemini but of longitudinal halves of chromosomes. In his prepared material there was no possibility of studying the heterotypic metaphase owing to poor fixation, nor could any accurate count of the chromosome number be made at anaphase. All stages of the homotypic division were missing in his material in spite of the fact that tetrads were formed. A chromosome count could not be made until the division in the pollen grain, and their number amounted to the reduced number, viz. 16—18. OEHLER adds (p. 671): »Die Reduktionsteilung vollzieht sich in den P.M.Z. offenbar noch ganz normal, die typischen Stadien der Synapsis und der Diakinese treten ohne sichtbare Abweichungen vom Typus auf».

After synapsis in the female organs a similar diakinesis is formed with 32—36 large chromosomes, all of which are thought to have already divided lengthwise. In the following metaphase the chromosomes are arranged in one plate (Pl. 3, Fig. 17). *There is no doubt*, although OEHLER does not consider it reductional, *that this figure shows a number of bivalents* with univalents strewn among them. This first division is followed by the interkinetic stage where each nucleus contains 32 chromosomes, *which are considerably smaller* than in the preceding metaphase (p. 691 and Pl. 3, Fig. 18). No examination of the chromosome number in somatic tissue was made. From this description of the course of meiosis it must therefore be considered improbable that *Cotylanthera* contains parthenogenesis of the *Alchemilla* type. It may be added here that SUESSENGUTH (1927) has observed germinating pollen tubes in the style.

Thismia javanica has been shown to have a tetrad division in the female organs, but ERNST, who in collaboration with BERNARD analysed this genus in 1910, an analysis which MEYER himself (1925) considers to be more complete than his own (1910), expresses the opinion that its parthenogenesis is problematic (1918, p. 324) and therefore the matter has not been elucidated.

Salomonia cylindrica was described by SHADOWSKY as parthenogenetic, although he, too, observed germinating pollen tubes in the styles. WIRZ and REISER have only observed sexual development (v. also ERNST, 1918, pp. 322 and 324). Owing to the previous erroneous count of the chromosome number, SÖDERBERG regards *Houttuynia cordata* as a sexual species. Compare however OKABE [1].

There remains *Artemisia nitida*, which according to CHIARUGI's excellent examination, exhibits in addition to the *Antennaria* and *Taraxacum* schemes also the *Alchemilla* scheme.

CHIARUGI claims that he has also observed in the male organs a process by means of which the tetrad cells obtain the zygoid number (cf. ROSENBERG, 1930, p. 52). Undoubtedly his pictures also show homotypic metaphases with 27 (2n) chromosomes in each plate. He is of opinion that metaphases with the zygoid number of chromosomes are occasionally formed after contraction stages, which are then followed by a second homotypic division. But in certain biotypes of *Taraxacum* there occurs a regular formation of P.M.C:s with an increased number of chromosomes, which (can) undergo two divisions in the normal manner. It is therefore possible that CHIARUGI has come across such a case, all the more as *A. nitida* is both male and female sterile. *His Figs. 21 a and b undoubtedly show*

[1] OKABE's work is not found in any of the Swedish libraries and therefore it has not been possible to examine carefully what he has written on this problem.

a P.M.C. formed from two P.M.C:s. This P.M.C. has arisen either by fusion or by the lack of wall-formation.

He considers that the *Alchemilla scheme* in the female organs is represented by two pictures (Figs. 49 and 65). The former shows a tetrad, the cells of which are considerably larger than the azygoid tetrad close by, the latter a dyad which, owing to the size of the cell, CHIARUGI considers to be zygoid. In neither case is it possible to count the chromosomes, but CHIARUGI's opinion on this point is probably correct. The criticism passed above on the interpretation of the behaviour of certain P.M.C:s is also applicable to the female organs, all the more as they are entirely superfluous. Also in the female organs of a biotype of *Taraxacum* (*T. dissimile*, GUSTAFSSON, 1935, p. 28) — in spite of the stabilized parthenogenesis — I was successful in one case in discovering a prophase with the double chromosome number and in another ovule numerous cells round the E.M.C., likewise with the chromosome number doubled. We thus see that not even in *Artemisia nitida*, which is nevertheless one of the best examples of the *Alchemilla* scheme, is there any evidence that two homotypic divisions (or homologues thereof) follow each other immediately.

This investigation has thus shown that the genus *Alchemilla* exhibits apospory of a generative type and is not parthenogenetic, and that the majority of other genera described as having the so-called *Alchemilla* scheme have already been eliminated from the parthenogenesis or do not stand the test of a thorough analysis. This implies that there is no longer any grounds for maintaining the old classification into *Alchemilla*, *Taraxacum* and *Antennaria* schemes. The scheme which is said to correspond to the Normal type of sexual species must be omitted from parthenogenesis. The only classification possible is that based on the manner in which the embryo-sac obtains the zygoid chromosome number.

Whether the daughter cell forming the gametophyte in *Alchemilla* is really the E.M.C. or whether a rare pseudo-homotypic division can occur, *Alchemilla* must be looked upon as forming a transition to the *Antennaria* scheme. An occasional development of lateral cells as far as diakinetic or interkinetic stages has been shown by BÖÖS (1924, p. 228) and by LILJEFORS (1934, p. 295) in *Sorbus*. The border-line case between somatic division and meiosis, which results in zygoid nuclei, is just the pseudo-homotypic metaphase. It is of great importance to mention that HURST (1931) has observed pseudo-homotypic divisions in *Rosa*, which presumably cause the apomixis of that genus.

6. THE MECHANISM OF ZYGOID PARTHENOGENESIS.

Zygoid parthenogenesis consists of three distinct processes: 1) *Zygotene pairing or chiasma formation is suspended* so that eugemini

are never or very rarely formed in the female organs. On the other hand, a high degree of geminus formation can take place in the male organs of both plants and animals, as well as in the sexual ovogenesis in partially parthenogenetic animals. 2) *The daughter nuclei obtain the zygoid number of chromosomes.* This can happen in at least three different ways, viz. by the origin of restitution nuclei, by pseudohomotypic metaphases and by the so-called somatic divisions. 3) *The egg cell develops by internal or external stimulation.* In the last case pseudogamy occurs if the stimulus is a pollen-tube or a sperm (in *Rhabditis*).

A. THE FAILURE OF BIVALENT FORMATION IN THE FEMALE ORGANS.

The majority of investigators of this problem, whether in plants or animals, are fairly agreed with regard to the formation of gemini in the female organs, although no comprehensive opinion has been pronounced (cf. the quite erroneous description of parthenogenesis in functional cells in DARLINGTON, 1932, p. 431). If parthenogenesis is stabilized the formation of bivalents also fails as a rule. It will suffice here simply to refer to JUEL, 1905; OSAWA, 1913; HOLMGREN, 1919; STORK, 1920; TAHARA, 1921; BELAR, 1923; ANKEL, 1927—1929.

In those groups in which facultative parthenogenesis occurs (e. g. *Allium odorum*, MODILEWSKI, 1930), or meiosis can be brought about in exceptional cases, no gemini are formed in the parthenogenetically determined cells. In the sexually adapted cells, on the other hand, gemini are formed rather frequently, but it has not yet been ascertained to what extent, in the totally apomictic genera, they consist of secondary associations. Fig. 121 *a* in CARANO's work (1922) shows a formation which resembles a terminal secondary association, nor is it located in the longitudinal direction of the spindle. According to STEBBINS's investigations (1932), *Antennaria* affords cases of non-stabilized parthenogenesis (v. p. 96). According to him, gemini are formed in the female sexual metaphases. But probably they are nothing but secondary associations. — »The chromosomes», he writes, p. 329, »gradually and irregularly move towards the poles, so that they are scattered over the whole length of the spindle. Non-disjunction is common, and paired chromosomes may be seen at both poles». This statement, like his figures, shows that true gemini are undoubtedly less common here than in the P.M.C:s, where a high rate of geminus formation can occur. BERGMAN (1935 b) shows that the

formation of true gemini is also diminished (or omitted) in the E.M.C:s of male *Antennaria alpina.*

SCHRADER's analysis of the course of meiosis in the hexaploid apomict of *Daphnia pulex* (1926) is of great value. The pseudosexual eggs externally resemble the sexual ones in the corresponding amphimict, but as in true parthenogenetic forms there is no reduction in number. Nor are males belonging to this apomict known.

In both kinds of parthenogenetic eggs no synaptic prophase is formed. In spite of this a varying number of associations are formed during the division. In the following metaphase plate, which is equational, the associations are gradually resolved, true bivalents are not found.

No doubt we have here an example of the formation of pseudogemini which do not arise by chiasma formation but appear first during prometaphase and metaphase. Figs. 5—9 show that the associations (mostly) have only one connecting link in the longitudinal direction of the chromosomes. Nor do any interstitial chiasmata exist. Before the metaphase plate is completed the associated chromosomes begin to be repelled again.

As in *Taraxacum* the chromosome homology (hexaploidy), in my opinion, causes the terminal affinity to result in an attraction between certain univalents and a fusion of their pellicles, which, owing to repulsion between the two spindle attachments, may later on be drawn out into the form of long threads. SCHRADER also states explicitly that both univalents and associations lie at first in different planes scattered over the whole of the spindle (semi-heterotypic metaphase). In the following equatorial plate, which is thus pseudo-homotypic, the spindle attachments of the univalents have divided. The result will be a still more powerful repulsion and a resolution of the associations. Judging from SCHRADER's account and figures, there is a great possibility of non-disjunction between chromatids, which I have assumed to be the cause of the origin of new forms within the parthenogenetic phanerogams.

On p. 14 SCHRADER (1926) writes: »On the basis of the foregoing, it is hardly necessary to say that I do not regard the formation of aggregates as part of a process of synapsis and pseudoreduction in the ordinary sense». Hence no primary pairing is present.

The parthenogenetic genus, in which the formation of eugemini in the female organs has been most closely investigated, is *Taraxacum.* As I have already dealt with the occurrence of secondary associations at metaphase in two papers, that phenomenon will not be discussed

here. — *What reasons have we for assuming that these pseudogemini have not arisen by the formation of chiasmata and thereby exchange of chromatid-segments?*

1) In those diakineses which have reached their climax, thus after the greatest amount of repulsion has been reached, it has not been possible so far to ascertain the occurrence of any sure pairing.

2) The associations are most numerous at the anaphases.

3) They vary in number.

4) The connections between the chromosomes in them are never more than one in number, whereas in the sexual forms examined and in the P.M.C:s there are often two such connections (chiasmata).

5) Interstitial chiasmata, which are common in male metaphases and occur also in the female organs of sexual biotypes, have never been observed.

6) Neither does the *Hieracium boreale* scheme occur, that is, metaphases with an occasional bivalent situated in the longitudinal direction of the spindle while the univalents are scattered over the spindle. Pseudogemini do not occupy such a position until the pseudo-homotypic metaphase.

7) Homotypic metaphases or anaphases with reduced numbers have not been observed.

Of these points — in addition to 1 — 4, 5 and 7 are of such strong probative force that there can hardly be any doubt at all that true gemini occur exceedingly rarely. It is certain that a varying rate of primary pairing, as in *Taraxacum praestans* ♂, for instance, does not exist.

What is the cause of this state of things?

BERGMAN (1935 a) has assumed that the cause of asyndesis in sexual plants, that is, the occurrence of solitary recessive genes, may also be the cause of the origin of the altered meiosis in male and female organs of parthenogenetic species. It has already been shown that there is no similarity between the two types of organs in this respect. A different mode of development has been forced upon macrosporogenesis and microsporogenesis in plants in the same manner as ovogenesis and spermatogenesis in animals. It does not hold good even for *Hieracium*. As BERGMAN himself points out, following ROSENBERG (1927), — assuming that this detail has been correctly interpreted, cf. p. 10 — the division in the P.M.C:s takes place earlier than in the sexual forms, whereas it occurs later in the E.M.C. But apart from that there is a marked difference. For while the divisions in the P.M.C:s

are of a widely different character (they belong to at least four different types), the division in the E.M.C. is either pseudo-homotypic or so-called somatic, the types characteristic of the P.M.C:s have not been observed.

Between the genically conditioned asyndesis observed hitherto and the failure of pairing in parthenogenetic diakineses there are also obvious differences. In asyndetic maize (BEADLE, 1931) there usually occur 0—2 gemini, but occasionally complete pairing is observed. In barley (EKSTRAND, 1932) the recessive factor, it is true, has an inhibitory influence on the entire formation of bivalents, but more particularly on one or two gemini. In *Viola orphanidis* (CLAUSEN, 1930), in which perhaps a recessive gene suppresses the formation of gemini in the male, but not in the female organs, there occurs, even if rarely, formation of gemini. Thus these cases show a marked agreement with the so-called *Hieracium boreale* scheme in the male organs, but not at all with the female diakinetic stages in *Taraxacum* and *Hieracium* and other closely investigated parthenogenetic genera. Hence there is no positive evidence in support of the view that parthenogenesis in *Taraxacum*, *Hieracium*, etc. is caused by solitary recessive genes. The hybridisation and the increased number most frequently found indicate instead that in many cases parthenogenesis is caused by complementary factors.

In animals the connection between polyploidy, heterozygoty and parthenogenesis is not quite so clear. Certainly several polyploid apomicts have been found (*Trichoniscus provisorius*, VANDEL, 1927; *Artemia salina*, ARTOM, 1928, and others), but no evidence has been brought forward to prove that parthenogenesis is directly correlated with polyploidy as in plants. That hybridisation, however, even among animals, can play an important rôle for the inducement of parthenogenesis has been shown by several investigators, as for instance, NABOURS, 1929; ROBERTSON, 1931, who assume that »Tettigid Parthenogenesis», which is probably however of an automictic nature (ANKEL, 1929, p. 346), is caused by complementary genes. That mutations can give rise to parthenogenetic biotypes with pseudo-homotypic division is proved by P. HERTWIG's discovery of an apomict formed as a mutation from a sexual line of *Rhabditis pellio* (1920). At one stroke the conjugation of the chromosomes at prophase was suspended altogether. Only one maturation division occurs. The similarity to the asyndetic mutants found so far in the phanerogams is only apparent, no varying pairing was observed. »Hier

können wir bei gleich alten Eiern stets 14 isoliert liegende Einzelchromosomen zählen» (p. 326).

The mechanism of bivalent formation is made up of two processes: zygotene pairing and chiasma formation, the former not necessarily giving rise to the latter. The omission of pairing in parthenogenesis can therefore be due either to the failure of zygotene pairing or to the failure of chiasma formation. Both possibilities are realized. In the majority of the *Taraxacum* apomicts no zygotene pairing occurs (cf. however SEARS, 1922), in *Erigeron annuus*, on the other hand, there is a great probability that it does. Zygotene pairing similar to that found in *Erigeron* probably occurs in *Aphis palmae* (DE BAEHR, 1920). At diakinesis-metaphase the chromosome pairing is resolved. »Comme nous le voyons, l'union entre les composants de ces chromosomes diacinétiques n'est pas très etroite» (p. 323). DARLINGTON (1932, p. 334) considers this pairing to be due to terminal affinity. There is, however, no grounds for that assumption (DE BAEHR, Figs. 6—7). According to DARLINGTON's own point of view, a repulsion between spindle attachments, when chiasmata have not been formed, can furnish the same pictures. Some spindle attachments must then have been terminal, others median. Such a position of the spindle attachments is common. Zygotene pairing should have been complete, while the chiasma formation has failed.

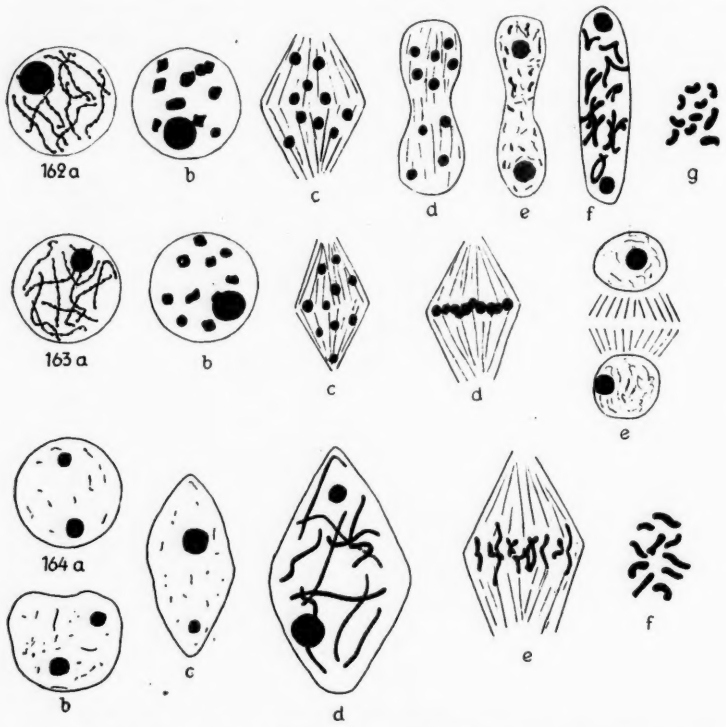
There are parallels to this failure of or decrease in chiasma formation among sexual plants. HUSKINS and SMITH (1934) observed that the zygotene threads in certain species of *Fritillaria* with localized chiasmata are, for the most part, already divided when the formation of chiasmata takes place (cf. DARLINGTON, 1932, p. 348). MC CLINTOCK (1933), in her studies of non-homologous association in maize, has shown that although such associations occur to a great extent between the zygotene threads, crossing-over takes place rather seldom, probably because the chromosomes do not lie close enough to each other. Something similar may of course be the cause of the failure of chiasma formation in the apomicts, although we have no definite information on that point. A failure of zygotene pairing may be due to the fact that the properties of the nuclear plasm have been altered in such a manner that the undivided chromosome threads do not attract each other. No elucidating investigations have been made so far on this fundamental question. In both cases however — as a comparison with the male organs will show — the failure of the formation of true gemini is no doubt due to physiological conditions.

B. THE FORMATION OF ZYGOID CHROMOSOME NUMBERS.

On p. 64 an account was given of processes which can give rise to zygoid embryos and yet — in my opinion — no parthenogenesis being present. Here a description will be given only of the three methods, which by means of an altered *but not omitted* meiosis effects the production of such embryos. Researchers who have studied the divisions in the female organs have in general regarded them as simply somatic divisions, that is, that the heterotypic division has been suppressed (for instance, STRASBURGER, 1909, p. 79; HOLMGREN, 1919, p. 107; STORCH, 1924, p. 380; ROSENBERG, 1927, p. 305, 1930, p. 54; ANKEL, 1929, pp. 367—368). JUEL, however, revealed uncommon discernment when he wrote already in 1905 p. 17: »Indessen sind die Verhältnisse in der E.M.Z.-Zelle von *Taraxacum* so einfach nicht, sondern vielmehr recht kompliziert. Diese Art hält offenbar, trotzdem dass sie apogam geworden ist, mit grosser Zähigkeit an den herkömmlichen Formen der Tetradenteilung fest». Later, THOMSEN (1927, cited from ANKEL) also rejected the prevailing view of the nature of parthenogenesis, that both maturation divisions can become rudimentary. »Das zähe Festhalten an mindestens einer Reifungsteilung, das die allermeisten Fälle von somatischer Parthenogenesis kennzeichnet, könnte doch darauf hindeuten, dass diese Teilung etwas mehr bedeute als eine bloss phylogenetische Reminiszens».

It can be asserted that of the three processes described below the first two are nothing but meioses, which, it is true, have resulted in the chromosome number being unreduced, but differ from the normal sexual meiosis only in the omitted pairing. DARLINGTON has shown that chromosome pairing and chiasma formation are not essential characteristics of meiosis, but that the difference between meiosis and mitosis lies in the cause of zygotene pairing and chiasma formation, viz. the different behaviour of their prophase chromosomes. The meiosis of the haplodiplonts prove the correctness of DARLINGTON's view. The course of the meiosis in biotypes with a variable degree of pairing, as for instance in *T. praestans* ♂, also shows that the occurrence of chiasma formation cannot serve as a characteristic feature of meiosis. Nor can a postulated zygotene pairing be employed as a basis of classification. Facts that speak against this are especially the behaviour of certain species and genus hybrids and the behaviour of the haplodiplonts. The cause of the dissimilarity between the two divisions must be associated with the failure or occurrence of reproduction of the chromosomes in the preceding stages.

As a result of the duration of the meiosis (zygotene pairing, chiasma formation, etc. before the metaphase movement) there is a greater contraction of the chromosomes at meiosis than at mitosis. Only a few of the parthenogenetic genera are characterized by a failure of contraction (*Antennaria*, *Hieracium*, *Eupatorium* ?, *Asplachna* ?). Nor



Figs. 162, 163 and 164. The formation of restitution nuclei, pseudo-homotypic metaphases and so-called somatic divisions in the E.M.C:s. See p. 81. Schematically drawn.

do »somatic» divisions alone occur in these genera, sexual and pseudo-homotypic metaphases arise besides them. Further, the prophases and the resting stages are not of a purely somatic nature.

The three methods of the origin of the zygoid number are illustrated schematically in Figs. 162—164. The first two show a strong chromosome contraction, the third exhibits chromosomes with a mitotic appearance.

The formation of restitution nuclei will be seen in Fig. 162 *a—g*. Following a failure of zygotene pairing (*a*) diakinesis (*b*) receives the zygoid number of univalents, which, after the resolution of the nuclear membrane, form a semi-heterotypic metaphase (*c*) with or without secondary associations. By the stretching of the spindle they are carried towards the two poles (*d*), a small number remain in the equatorial plate. All elements are enveloped in an interkinetic nucleus by the rise of a nuclear membrane around the spindle (*e*). The following homotypic metaphase (*g*) has the normal appearance and gives rise to a dyad with the zygoid chromosome number. One of the dyad cells (if a wall is formed) or both nuclei (if no wall is formed) then give rise to the embryo-sac.

The first stages of *the pseudo-homotypic metaphase* in *Taraxacum* and others (Fig. 163) are identical with corresponding stages in the preceding process. Owing to the failure of the spindle to stretch and the failure of a nuclear membrane to form, the spindle attachments of the univalents are able to divide and the chromosomes, as a result of their bipolarity, actively move towards the equatorial plane, where the halves separate. The result will be daughter nuclei with the zygoid number. Cell-walls can be formed or fail to form.

The pseudo-homotypic division in *Hieracium* and others is partly of a different kind. The character of the resting stages is the same as in the so-called somatic division (Fig. 164 *a—c*). The prophases contain long but rather thick chromosomes (v. Figs. 134—139), which do not acquire the spherical appearance until metaphase.

The *so-called somatic division* involves a retardation of the onset of prophase. The resting nucleus is characterized by an intense hydration of the chromosomes. In the succeeding prophase (Fig. 164 *d*) the unpaired chromosomes have a mitotic appearance. At metaphase (*e—f*) the chromosomes are certainly somewhat contracted but not so much as in Figs. 162 *c* and 163 *c*. At metaphase—anaphase (*e*) the two halves of each chromosome move towards the poles. The result even here will be two zygoid nuclei, between which no cell-wall is formed (?).

All three processes occur in the female organs of parthenogenetic plants. The pseudo-homotypic division, which is to a certain extent identical with FEDERLEY's *Pygaera* type, generally occurs in the female organs of parthenogenetic animals. No restitution nuclei have been observed so far in parthenogenetic animals. According to STORCH (1924) a »somatic division» occurs in *Asplachna*, but his own results are contradictory, and other investigators have obtained different results

(TAUSON, 1924; MARINELLI, 1925, according to ANKEL, 1929). According to earlier investigations the genus *Neuroterus* is said to exhibit a complete loss of the meiosis. Compare, however, p. 68.

In the male organs of parthenogenetic plants restitution nuclei are of the most common occurrence. Pseudo-homotypic metaphases occur in *Taraxacum maculigerum*. The P.M.C:s of *Hieracium* have divisions that often show a »somatic» tendency (ROSENBERG), purely somatic divisions have been observed in *H. lapponicum*.

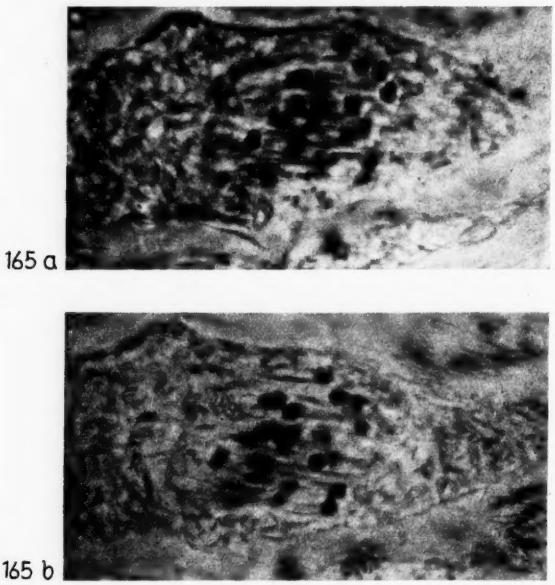


Fig. 165. A microphoto of Fig. 25 *b*. In *a* the association at the top right hand corner has a small but plainly visible connecting thread, in *b* two associations can be seen at the lower part of the plate. — 2400 ×. Photo O. MATTSSON.

The first two types have been shown to occur in the male organs of haplodiplonts (BLEIER, 1933) and also in species hybrids with complete failure of geminus formation (e. g. FEDERLEY, 1912; KARPECHENKO, 1927). The pseudo-homotypic division appears to be much more common among animals than among plants (owing to the different capacity of the spindle to stretch?). No cases of completely »somatic» maturation division have been observed in sexual biotypes; on the other hand, the »precocity» can be altered to such an extent that

solitary or even all the chromosomes do not contract as in normal meiosis (PHILP and HUSKINS, 1931).

a. *The Formation of Restitution Nuclei and its Causes.*

The significance of restitution nuclei for the origin of doubled chromosome numbers was made clear by ROSENBERG in 1927. But we have no definite information about the condition which causes them. ROSENBERG was of opinion that in *Hieracium* they were quite simply caused by the semi-heterotypic division, which brings about an uneven distribution of the univalents over the whole of the spindle, so that at anaphase—telophase a nuclear membrane is formed round all the chromosomes (Case 1). In certain species of *Prunus*, in which restitution nuclei have been found, DARLINGTON (1930) considers them to be due to laggards at anaphase (Case 2). These explanations — which are of course at bottom identical — constitute however only an apparent solution.

The univalents in a heterotypic metaphase have no power of their own to move until the attachments have divided (BLEIER, 1931, 1933; DARLINGTON, 1932; GUSTAFSSON, 1934 c, 1935). It has been ascertained (GUSTAFSSON, 1934 c) that the univalents in *Taraxacum* biotypes with a low rate of geminus formation seldom move towards the equator and divide there, instead they become entirely incorporated with the daughter nuclei or form small nuclei. In biotypes with high pairing they often divide already at first metaphase. The works of BELAR and DARLINGTON (1928 and 1932) have furnished evidence of the probability that the nuclear spindle in the course of anaphase stretches. Even by this means the gemini chromosomes are moved apart and any possibly undivided univalents are passively driven towards the poles. This view has for several reasons been accepted as applicable also to *Taraxacum* (GUSTAFSSON, 1934 c, 1935).

There is a marked difference between the constancy and appearance of the restitution nuclei in male and female organs in Taraxacum. In the female organs the restitution nuclei have mostly the same appearance, thin and elongated as already described by JUEL (1905) and confirmed by later investigators. In the P.M.C:s, however the restitution nuclei vary very much in appearance. Microphotographs 166 *a—f* and Figs. 37—42 show some different types.

But this is not the most important difference. Table 9 shows that the restitution nuclei of the male organs often are incomplete. Owing to the fact that the semi-heterotypic anaphases in *Taraxacum* always

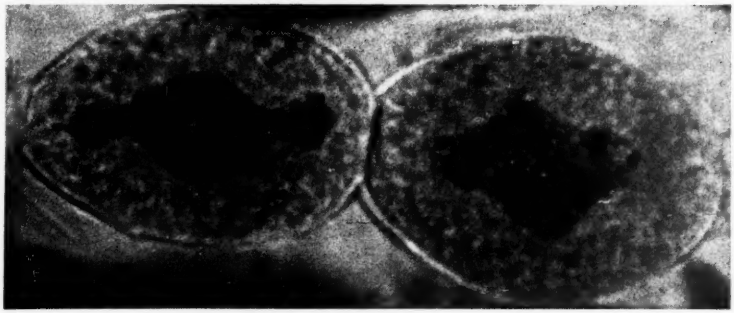
exhibit an equal distribution of the chromosomes to the two poles, I have in the triploid biotypes considered restitution nuclei to occur when the homotypic metaphases show at least 19 chromosomes in one plate. The apomicts listed are representative of all material investigated.

TABLE 9. *The Formation of Restitution Nuclei in Taraxacum Apomicts.*

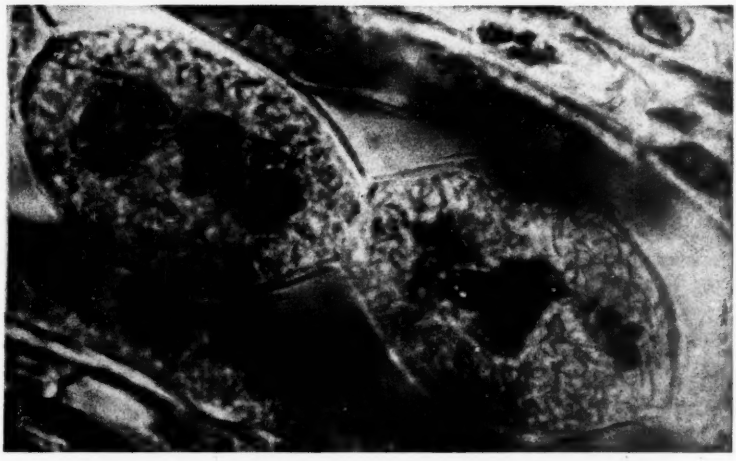
Apomict	No. of cases	Formation of complete restitution nuclei	Formation of restitution nuclei with isolated chromosomes						
			1	2	3	4	5	chrom.	%
T. praestans ...	111	76	17	9	4	3	2	= 35	32
T. maculigerum	117	68	27	16	3	1	2	= 49	41
T. tenuilobum	43	32	5	2	1	—	3	= 11	26
T. alpinum (× *Pacheri*?) ...	15	10	1	2	1	—	1	= 5	33
Total No. of cases		186	51	31	12	8	13	= 100	35 %

None of the investigators, however, who have worked on the development of the female organs in *Taraxacum*, have observed more than one homotypic metaphase in the E.M.C., nor found any isolated chromosomes, triads or tetrads. SEARS thus says (1922, p. 318): »Inspection of hundreds of embryo-sacs failed to disclose tetrad formation». Undoubtedly the parthenogenesis in *Taraxacum* is stabilized. Several hundred heterotypic metaphases and anaphases, pseudo-homotypic and homotypic metaphases and an equal number of recorded dyad stages have been examined without any possibility to find isolated chromosomes outside the daughter nuclei or more than one homotypic spindle.

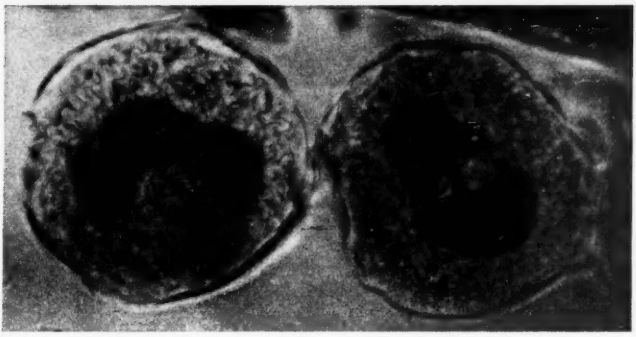
In a previous paper (1935, p. 19, Fig. 52) I described a case in the female organs where the formation of restitution nuclei could be studied at »the moment of birth». The inference was drawn that the stretched spindle forms the restitution nucleus in the E.M.C. Only in this way can a restitution nucleus arise, having the characteristic elongated shape and all the chromosomes incorporated. »The picture also shows that the restitution nucleus is limited and is formed (by »precipitation») of the spindle. The membrane therefore develops at no great distance



166 a-b



166 c-d



166 e-f

Fig. 166. *T. praestans* LINDB. fil. — Six different types of restitution nuclei, *d* resembling that of Fig. 39, *f* a hollow nucleus like that of Fig. 42. — 2400 ×. Photo O. MATTSSON.

from the solitary chromosomes, on the contrary several of them can be seen in close proximity to the developed wall. The regularity in the formation of restitution nuclei in the E.M.C. in this way acquires its natural explanation. — For if the method of origin and the shape of restitution nuclei are induced by the spindle itself it is hardly possible for any irregularities to occur, which prevent isolated chromosomes from being embodied in the nucleus. This is in marked contrast to the state of things in the P.M.C:s where even the formation of restitution nuclei is often of a degenerative nature.»

That the formation of restitution nuclei is even here often associated with the stretching of the spindle is shown by the numerous pictures of hourglass shaped nuclei found in the literature (v. also ROSENBERG's Fig. 3 *D*, 1927, which shows an anaphase with a stretched spindle). But in order to explain the existence of incomplete restitution nuclei we must assume that in some way or other the chromosomes glide outside the spindle or that *the nuclear membrane is not formed at the outskirts of the spindle but within it at varying distances from the periphery.* The occurrence of isolated chromosomes and the irregular shape of the restitution nuclei may only be explained in the second manner. The »precipitation», occurring at the outskirts of the stretched spindle in the E.M.C., must take place at varying points of the spindle in the P.M.C. Even the extreme case, where nuclear membranes arise round solitary gemini, has been observed (p. 14). A nuclear membrane can also arise in such a manner that the central part of the cell is not incorporated with the newly arisen nucleus (Fig. 38).

If the change in the spindle, which leads to the formation of a nuclear membrane in or around it, is an inherent specific property, then what causes the change in question? Is it the univalence that brings it about? This phenomenon need not by any means be correlated with the formation of restitution nuclei. Otherwise restitution nuclei should be produced to a much greater extent after the semi-heterotypic divisions, and should besides be equally numerous in different biotypes. Table 10 gives the dyad formation in some apomicts with semi-heterotypic divisions, variable or constant pairing. A very large number of restitution nuclei is found in *T. 1930:662*, formation of gemini unknown. *T. palustre* coll. is characterized by a large number of dyads although up to 6 gemini occur. *T. 1929:8*, on the other hand, lacks mostly every trace of gemini. *The percentage of dyads must therefore be considered to vary in different biotypes and is not dependent on the percentage of semi-heterotypic metaphases.*

There is no necessity either of univalence being associated with any formation of restitution nuclei. This is shown by STEBBINS's investigations of *Antennaria*. While restitution nuclei are by no means rare in the male organs of the hermaphrodites (in *A. canadensis*, which has a few bivalents and 70—80 univalents, dyads are formed at the rate of 25 %—37 %), no such nuclei occur in the females in spite of the fact that semi-heterotypic metaphases with solitary bivalents (?)

TABLE 10. *Dyad and Polyad Formation in Taraxacum Apomicts.*

Apomict	No. of cases	Dyad formation	Polyad formation (> than four cells)	No. of gemini
1930 : 662	280	87 %	0,4 %	0?
T. apollinis	360	64 %	0,3 %	?
T. palustre coll.	346	53 %	0,8 %	0—6
T. praestans	186	30 %	17 %	0—9
1928 : 8	146	28 %	8 %	0(—2)
T. amborum	252	25 %	12 %	0—8
1929 : 19	255	21 %	8 %	0—6
1929 : 5	290	13 %	48 %	High?
1930 : 287	393	12 %	2 %	?
1930 : 302	300	12 %	17 %	3—13
T. Samuelssonii	159	5 %	13 %	9
T. alpinum coll.	243	2 %	4 %	High
T. 1930 : 688	195	1 %	45 %	?
T. Kalbfussi	95	0 %	24 %	8

are formed in certain cases in as much as 25 % of the ovules. »At the heterotypic metaphase there are a few chromosomes at the equator, but the majority are scattered irregularly over the spindle. — At the heterotypic telophase a large mass of chromatin at the center of the spindle is left out of the two daughter nuclei, and forms a third nucleus. — This division results in a hexad, although slight irregularities in it frequently cause the presence of small extra nuclei» (1932, p. 328—329).

The same phenomenon is seen in the P.M.C:s of *T. lanceolatum*. At the heterotypic metaphase this tetraploid apomict has, it is true, 4 gemini on the average, but at the anaphases, as shown in Figs. 87—89, univalents forming bridges are regularly met with. Although the two anaphase plates are connected by a large number of chromosomes no restitution nuclei ever arise. At the homotypic metaphase 2—3 plates are seen in each P.M.C. in addition to a number of isolated univalents in the cytoplasm (Table 11). Polyads are formed instead of restitution

nuclei. The polyad formation occurring in many other apomicts (in *1929*:5 and *1930*:*688* amounting to 48 % and 45 % respectively) is probably explained in the same way. At metaphase-anaphase numerous univalents occur in them but in spite of that no restitution nuclei, or very few, are formed. The case is just the reverse between the frequency of the formation of polyads and the formation of restitution nuclei. If polyads are formed in large numbers no formation of restitution nuclei takes place. If the latter is high considerably fewer polyads arise.

TABLE 11. *Tetrad Formation with Appertaining Phenomena in T. lanceolatum.*

1) No. of »tetrad cells» in each P.M.C.	1	2	3	4	5	6	7	8	
No. of cases	—	(1?)	19	59	8	9	1	1	= 98
2) No. of homotypic spindles	1	2	3	4					
No. of cases	—	47	7	—					= 54
3) No. of groups to which the chromosomes have been distributed ..	1	2	3	4					
No. of cases	—	28	35	16					= 79
4) No. of isolated chromosomes in homotypic stages	1	2	3						
No. of cases	17	14	6						= 37

Those *Taraxacum* biotypes, which like DARLINGTON's species of *Prunus* have a number of lagging univalents at the heterotypic anaphase but at the same time have constant pairing, demonstrate that even this phenomenon is not necessarily associated with nuclear restitution. The species carefully investigated in this respect are *T. Nordstedtii* and *T. Kalbfussi* (GUSTAFSSON, 1935, p. 4—6). At the male meiosis the former has one or more univalents, which often become divided in the equatorial plane, the latter has regularly at least 6—8 univalents, which are sometimes divided at anaphase. In spite of that restitution nuclei are never formed. Later a third biotype, *T. melanthoides*, was studied. This biotype has up to 10 gemini, one or two of which, at most, form trivalents, sometimes not more than 7—8 gemini are found. Fig. 58 shows an anaphase with 8 lagging univalents. Such P.M.C:s are numerous. *No restitution nuclei, however, have been observed.* Instead the univalents form small nuclei. Thus in these three apomicts the nuclear membrane is not formed round all the chromosomes, being formed instead round the two daughter plates separately and in a varying degree round the univalents.

Thus the formation of restitution nuclei is not entirely due to the univalence, as has been maintained hitherto, but in some way or other is only correlated with it, in the same way as failure of pairing is correlated with lack of homology but is not necessarily caused by it. Univalence is, so to say, the basis on which the altered properties of the spindle may find expression. Of the physiological conditions which cause these changes we know nothing.

That restitution nuclei can also arise in cells in which lagging univalents or univalent halves are wanting is evidenced by the so-called pseudo-amitoses in somatic tissue. An interesting case of a regular somatic increase in the chromosome number is mentioned by MEURMAN (1933) in *Acer platanoides*, which does not exhibit any other abnormalities. According to MOFFETT's investigation (1932) such abnormalities are however found in *Kniphofia*. Here the increase is correlated with abnormalities in the development of the spindle at meiosis.

To summarize it may thus be said that the formation of restitution nuclei in sporogenesis is correlated with the univalence of the chromosomes, but is not due to it, being caused instead by the spindle itself. In the female organs of *Taraxacum* a nuclear membrane is formed at the periphery of the spindle at the same time as or shortly after the stretching of the spindle, all the chromosomes are incorporated and restitution nuclei fail only in the ovules in which the pseudo-homotypic division occurs. In the male organs, on the other hand, a nuclear membrane is formed — if the presence of isolated chromosomes is to be satisfactorily explained — within the spindle, so that solitary chromosomes frequently lie outside the restitution nucleus. The physiological conditions causing this »different precipitation» in the spindle vary in different apomicts so that apomicts with an identical type of division have varying percentages of dyads.

b. *The Mechanism of the Pseudo-homotypic Division.*

The pseudo-homotypic division is essentially identical with the *Pygaera* type in sexual species, where the chromosome pairing has failed but the chromosomes nevertheless directly form a heterotypic plate. The mechanism of this process is simple: The spindle does not begin to stretch until the spindle attachments have divided, whereby the univalents become bipolar and behave like gemini. In the equatorial plane, where they accumulate, the halves are separated.

Even in this case the spindle is therefore of a certain importance.

The stretching of the spindle must take place after the division of the univalents. This alteration in time may be due to two causes:

1) The attachments divide earlier than at metaphases with attendant restitution formations. The spindle *has no time* to stretch.

2) The attachments divide at the normal time but the stretching of the spindle *takes place* (at the same time as or) *later* than in sexual meioses with complete bivalence, much later than at divisions in which restitution nuclei arise.

The different behaviour of the semi-heterotypic metaphases, whereby they can partly pass into anaphases, partly into pseudo-homotypic metaphases, proves that the spindle is independent of the character of the division, and thus furnishes evidence of the important task assigned to it here in accordance with the conclusions drawn by BELAR and DARLINGTON. In both cases total univalence (apart from possible secondary associations) occurs in the female organs. There are no grounds for assuming that the pseudo-homotypic division is caused by an earlier division of the spindle attachments. The semi-heterotypic metaphases have the same appearance whatever may become of them, which is also true of the chromosomes.

The duration of diakinesis — anaphase in semi-heterotypic divisions with accompanying formation of restitution nuclei is therefore shorter than in normal meioses with complete bivalence and in these again shorter than in the pseudo-homotypic divisions. For in normal meioses the bivalents are bipolar when they enter metaphase, thus they require only sufficient time to become arranged in the plate. At the semi-heterotypic metaphases only unipolar elements are present. If the spindle stretches, then anaphase is formed. If no stretching of the spindle takes place the attachments will sooner or later divide and the result will be the pseudo-homotypic metaphase.

Even with respect to the pseudo-homotypic metaphase there is a marked difference between male and female organs in *Taraxacum*, for in the former pseudo-homotypic division has been observed in only one apomict, *T. maculigerum*. The nature of the division, however, was not the same in the P.M.C:s of this biotype as in the ovules. The univalents appear divided lengthwise so that the halves do not lie close to each other, and there occurs a slight contraction of the chromosome mass. Is this difference in appearance due to the earlier division of the univalents? Is not the failure of the spindle to stretch, as in the female organs, the cause of this divergent pseudo-homotypic division?

An important conclusion is to be drawn from the fact that *res-*

titution nuclei never arise when the pseudo-homotypic metaphase is in process of formation or has been formed. For this proves that the restitution nuclei in the E.M.C:s are necessarily associated with the stretching of the spindle. At the pseudo-homotypic anaphase no nuclear membrane is ever formed round both plates. The physiology of the spindle is therefore different in the two kinds of anaphases.

It is also conceivable that an unequal percentage of restitution nuclei, in proportion to the percentage of pseudo-homotypic metaphases, should be met with in *Taraxacum*. No evidence can yet be furnished with regard to this question. The behaviour of different genera, however, proves the possibility of this conception. In *Balanophora japonica* only restitution nuclei occur (?), in *Taraxacum*, *Chondrilla* and *Erigeron mucronatus* (?) restitution nuclei and pseudo-homotypic divisions have proportionatly the same frequency, in *Erigeron annuus* and *E. ramosus*, *Hieracium*, *Antennaria* and in most animals restitution nuclei do not occur in the female organs. The occurrence of these two types of division is probably regulated by the different behaviour of the spindle in each separate case.

c. *The so-called Somatic Division in the Female Organs.*

Careful investigations have revealed that a division of a »somatic type» in place of the meiotic division is considerably rarer than was considered to be the case formerly. Metaphases with uncontracted chromosomes have been met with only in *Poa* and *Antennaria*. *Hieracium* and *Erigeron* exhibit prophases which are undoubtedly indications of its existence. In the last three genera pseudo-homotypic metaphases also occur, almost always in *Erigeron* and preponderantly in *Hieracium*. The proportion of pseudo-homotypic divisions to so-called somatic divisions in *Antennaria* is not known. HOLMGREN's statements with regard to *Eupatorium* are not quite explicit. He says that after diakineses with elongated chromosomes — but not so elongated as in the pseudo-homotypic prophases in *Hieracium* — the chromosomes »again become rather short», as in *Taraxacum* and *Antennaria* (according to JUEL's investigation in 1900). Whether this statement is to be understood as evidence of the occurrence of the pseudo-homotypic metaphase is perhaps not quite certain. In *Asplachna*, STORCH has observed metaphases with round chromosomes, but he nevertheless considers the chromosomes to be elongated in shape and that their round appearance is due to an optical illusion (!).

In *Antennaria*, *Hieracium* and *Eupatorium* the resting stages and

prophases — apart from the sexually adapted ovules — are identical in character, but in *Hieracium* pseudo-homotypic divisions are nevertheless produced for the most part. Hence there is no doubt that the two types of divisions are here interwoven. This is probably true also of the other two genera.

The female parthenogenetic E.M.C:s of the three genera are characterized by the following features:

1) A long delay in the onset of prophase (JUEL, 1900, p. 20; HOLMGREN, 1919, p. 84; STEBBINS, 1933, p. 327; BERGMAN, 1935 a, p. 58; GUSTAFSSON, 1934 b and the present work).

2) The »chromatin lack» of the resting nucleus. In staining with gentian violet or haematoxylin the nuclear cavity is practically unstained.

3) The intense growth of the cell and the resting nucleus, as compared with that of the sexual E.M.C:s, so that they increase more than three or four times in volume.

4) The irregular growth of the resting stage whereby varying shapes arise (v. p. 44; also HOLMGREN, Fig. 18 b and c).

5) The varying time of onset of the prophase in different ovules. The variation in this respect is considerable in *Hieracium*.

6) The rapid carrying through of both the pseudo-homotypic division and the »somatic» one.

7 a) The chromosomes are certainly elongated, and their length is considerably greater than their breadth, but they are nevertheless broad as at the heterotypic prophases in many sexual plants. Such prophases with elongated chromosomes have also been observed in the male organs of *Hieracium* apomicts (ROSENBERG, 1927, *H. laevigatum*).

7 b) The chromosomes suddenly develop into the form of long, slender threads. No preceding stages like the »spireme» in vegetative cells have been observed however.

8 a) The chromosomes contract into a spherical shape and, as in *Taraxacum*, *Chondrilla* and *Erigeron*, form a pseudo-homotypic metaphase. This certainly takes place in *Hieracium* and probably also in an analogous form in *Antennaria* and *Eupatorium*.

8 b) The chromosomes remain to a certain extent uncontracted at metaphase and form a »somatic» plate. This has only been observed in *Antennaria* (and *Poa*).

The unusually intense hydration of the nuclei in the three genera mentioned above and in all species investigated furnishes — in my opinion — the explanation of these unique conditions. The sexual

species do not reveal the same phenomena (cf. for example HOLMGREN, p. 84). Thus there is no doubt that retardation of the division and the intense hydration of the chromosomes are correlated with each other.

The chromosomes are hydrated so intensely at the beginning of the resting stage following premeiotic anaphase that when stained they do not show off so well against the remainder of the nuclear contents. Even for this process a longer time is of course required than that usually occupied by somatic or meiotic divisions. The result of this will be that the cell and nucleus have time to grow beyond the normal size before the resting stage has come to an end. As shown by the findings in *Hieracium*, the duration of the resting stage does not necessarily cause a change in the character of the division. If the resting stage is too long such a change may, however, take place, rarely in *Hieracium* but more commonly in *Antennaria* (?).

The variation in the time at which prophase sets in in the various ovules is evidence in proof of this. Hydration varies from case to case, and that is the cause of the variation in the time of the onset of the divisions. This view also furnishes the simple explanation of the rapid carrying through of the prophase—telophase.

Germination tests made in *Hieracium* have shown that in certain cases up to 50 % of achenes with contents — thus not parthenocarpic — lack the power to break through the pericarp. This is because the development of the pericarp and that of the embryo do not run parallelly, so that the former is often completed while the embryo is still in an early stage of development. Owing to the very great retardation of the »somatic» division this 50 % defective or parthenocarpic achenes includes those achenes of *Hieracium* which show this type of division. Perhaps the division itself is also an expression of a degenerative phenomenon caused by the advanced age of the nucleus or its »death convulsion».

C. THE DEVELOPMENT OF THE PARTHENOGENETIC EGG-CELL.

In his work published in 1923, HABERLANDT asserts that necrohormones from dying cells in the neighbourhood of the parthenogenetic E.M.C. play a stimulating rôle with regard to the course of meiosis in a so-called somatic direction. This view has been criticized, quite correctly in my opinion, by several investigators (MEYER, 1925; SCHÜRHOFF, 1926; ROSENBERG, 1930; PODDUBNAJA-ARNOLDI, 1933). In spite of fairly extensive examinations of E.M.C:s in *Taraxacum* apomicts, I did not succeed in finding any dying cells in their proximity.

There is no doubt that the condition of the nucleus is determined long before diakinesis and metaphase, in fact already during the resting stage (the failure of the division of the chromosome threads).

The problem of the development of the egg-cell is somewhat different. In the parthenogenetic apomicts a distinction must be made between the processes by which the progenies of the E.M.C:s acquire the zygoid chromosome number and the stimulation which causes the development of the egg-cell. That this distinction is correct is shown, among other things, by the cases in which the zygoid embryo-sacs, whether parthenogenetic or aposporous, of *Gastrodia elata* (KUSANO, 1915), *Artemisia nitida* (CHIARUGI, 1926), *Ochna serrulata* (CHIARUGI and FRANCINI, 1930) do not contain any egg-cells capable of development in spite of their being quite normal. Multiplication takes place instead in the first case by means of normal fertilisation, in the second by rhizomes, in the third by adventitious embryos. Neither in sexual species, in which the egg-cell for some reason or other has obtained the zygoid number, does it develop without fertilisation.

It is not impossible that HABERLANDT's view supplies the explanation of the development of the egg-cell. In *Oenothera Lamarckiana*, HABERLANDT has indisputably succeeded in showing that adventitious embryos are produced by injury (1921 a); in the parthenogenetic *Marsilia Drummondii* a corresponding stimulation can be thought to proceed from the dying ventral canal-cell (1922), and it is not inconceivable that dying cells around the parthenogenetic egg-cell (synergids, etc.) can cause its development (1921 b).

The discoveries of pseudogamy seem to confirm the correctness of HABERLANDT's point of view. To ensure further development it is necessary in these cases (many genera of the *Rosaceae* (?), *Atamosco*, *Rhabditis*) that foreign stimulants act upon the egg-cell. But in the last case this influence is of an entirely different kind from that imagined by HABERLANDT. In *Atamosco* (PACE, 1913) one sperm-nucleus in the cytoplasm of the egg-cell degenerates and the other fuses with the two polar nuclei and forms an endosperm, which is pentaploid. It is only in this way that an embryo can arise. In certain species of *Rhabditis*, BELAR (1924) was able to ascertain that fertilisation is necessary in spite of the fact that nuclear fusion never takes place. Instead the entering sperm degenerates after having supplied a centrosome to the egg-nucleus, which then divides in the usual manner (merospermy). In the last case foreign substances do not

stimulate development chemically and thus HABERLANDT's view is not correct.

The omission of pairing in the early stages of the E.M.C:s is not determined from without but is an autonomic phenomenon in the nucleus. *Probably the development of the egg-cells is in most cases also autonomic and is not determined by any stimulation from dying cells in the neighbourhood.* This is proved by the simultaneous occurrence of many zygoid gametophytes in *Artemisia* and *Ochna*. The chance of one of the synergids beginning to degenerate earlier than the egg-cell or of surrounding embryo-sacs, already dead, sending out necrohormones, is of course very great. Nevertheless no development takes place.

7. STABILIZED AND UNSTABILIZED PARTHENOGENESIS.

TÄCKHOLM (1922) considered that he was able to ascertain that sexual segregation products are never formed in parthenogenetic apomicts within the genera *Taraxacum*, *Hieracium* and others. Are never azygoid fertilizable, as well as zygoid parthenogenetic, egg-cells formed in cases of unstabilized parthenogenesis?

Cases of unstabilized parthenogenesis occur where zygoid embryo-sacs arise, but still multiplication takes place in another manner. *Artemisia nitida* and *Ochna serrulata* exhibit two such cases. The former species is an alloploid which does not produce any agamospermous seeds but multiplies by means of rhizomes. In spite of this — or associated with it — it exhibits a miscellany of various agamospermous phenomena.

The E.M.C:s show in regard to meiosis the same irregularities as the P.M.C:s. 1) Complete formation of gemini (13 in number) can occur. 2) Semi-heterotypic diakinesis and metaphase arise, the chromosomes being distributed at random to the two anaphase plates. 3) Restitution nuclei are probably formed. 4) Occasionally diakineses with elongated »undivided» chromosomes are produced and undergo a normal equational division. 5) Embryo-sacs are produced according to the »*Antennaria*, *Taraxacum* and *Alchemilla* schemes». After macrospore formation the nucellus is found filled with nuclei of varying sizes in process of degeneration. Occasionally cells in the nucellar epidermis or chalazal region are enlarged, enter the nucellar cavity, displace the macrospores and form aposporous embryo-sacs. After the degeneration of the mature embryo-sacs vegetative cells or undeveloped macrospores may again develop into new gametophytes, which manifest numerous abnormalities.

The pentaploid, probably autoploid, *Ochna serrulata* shows agamospermy of a similar multiple nature: zygoid parthenogenesis, apospory and adventitious em-

bryony. Embryos arise only by the development of an epidermic cell from the integument in the proximity of the micropyle.

According to STEBBINS's investigations, *Antennaria* provides interesting instances of unstabilized parthenogenesis.

In the few »males» examined, meiosis in the P.M.C:s shows a varying number of bivalents and univalents, in *A. canadensis* (2n = 84) about 80 univalents occur. In all individuals restitution nuclei occurred more or less frequently. Achenes are also formed in the »males» (in *A. fallax* in 2 %—25 % of the ovules).

The females exhibit two quite different phenomena in the E.M.C:s. In one of them the division is not retarded, synaptic contraction takes place and at the diakineses both bivalents and univalents are seen. At metaphase they lie scattered over the whole of the spindle. During anaphase the spindle stretches greatly (p. 329 and Figs. 9—11). At first telophase the chromosomes are distributed among three nuclei. Thus the homotypic metaphase contains more than two plates. Pentads, hexads, etc. are formed. Embryo-sacs that have arisen in this way sometimes degenerate early. Embryos are probably never formed by fertilization. The most important point is that in spite of the stretching of the spindle no restitution nuclei have ever been observed in these divisions. In *A. occidentalis* (2 individuals examined) these divisions occur in 25 % of the E.M.C:s, in *A. fallax* only in one of two individuals, in *A. Parlinii* (4 individuals examined) they seldom occur. In 5 individuals of *A. canadensis* only one case of reduction was observed, in one of two individuals of *A. petaloidea* examined reduction in chromosome number occurred in 20 % of the cases, whereas they never occurred in the other. In *A. neodioica* such reductional divisions were found in one of three individuals (10—15 %), whereas they were never found in var. *attenuata*. One reductional division was discerned in an individual of *A. Brainerdii*.

The other type has already been described. Nucleus and cell grow abnormally. »As the nucellar cells start to degenerate the nucleus moves out to the micropylar end of the young embryo-sac. When most of the nucellar cells have degenerated and the embryo-sac has pushed out beyond them, this mother nucleus divides for the first time. This division is carried through very quickly, and its stages are difficult to find» (p. 327). The following metaphase shows mitotic chromosomes. Occasionally pseudo-homotypic metaphases are formed. »Here the chromosomes are much smaller than in the usual type of metaphase, and are comparatively shorter and thicker» (p. 331). No information is given as to the number of metaphases with mitotic chromosomes observed. They may have been only one? *Particular attention must be called to the marked degeneration of the nucellus before the prophase begins.*

Isolation experiments on *A. occidentalis* showed 50 %—56 % developed achenes, in the other species they varied between 50 % and 80 %. From this it is evident that in addition to ovules having reductional division *there are also a large number* (20 %—50 %) *of ovules of the »Hieracium type» which do not develop.* To what extent the mature achenes are germinative no information is given.

Judging from HOLMGREN's account, parthenogenesis is fully

stabilized in *Erigeron ramosus* and *Eupatorium glandulosum*. In its first division *E. glandulosum* has the *Hieracium* type, probably with pseudo-homotypic metaphase. No ovules with early divisions were observed.

In *Chondrilla* species PODDUBNAJA-ARNOLDI could in many cases record more than two nuclei and cells in the female dyad stage. This is probably associated with a disturbed formation of nuclear membrane at anaphase as in the P.M.C:s in *Taraxacum*, so that incomplete restitution nuclei arise.

In *Ch. pauciflora, acantholepis, juncea, graminea, coronifera, brevirostris* 1, 2, 3, regular dyads are formed at the rate of 94, 94, 95, 68, 77, 63, 88 and 96 per cent. respectively. Thus different individuals of the »same apomict» (*brevirostris*) have varying ratios. In *Ch. pauciflora, acantholepis, juncea, graminea, brevirostris* 2 and 3 and *ambigua* (sexual) mature achenes were produced by 92, 93, 78, 94, 84, 90 and 98 per cent. of the flowers. The formation of achenes and dyads is perhaps influenced by external factors. Up to 90 per cent. of the pollen is sterile.

The cytological examination of *Taraxacum* has never shown for certain (except in one case) other than dyads. Homotypic metaphases always consisted of only one plate, no isolated chromosomes or small nuclei occurred. Hence parthenogenesis is stabilized. An examination of the mature heads, however, shows failure of fruit-bearing in 0—12 per cent. of the cases (Table 12). Probably this condition is due to a phenotypically or genetically caused lack in the supply of nutrition or the space in the heads.

TABLE 12. *Achene Production in Taraxacum Apomicts.*

	Mature Achenes	Undeveloped Achenes	Percentage of Undeveloped Achenes
T. Nordstedtii	170	3	1,7
T. maculigerum	191	16	7,7
T. platyglossum	239	8	3,2
T. balticum	324	33	9,2
T. Kalbfussi	70	2	2,8
T. semiglobosum	254	36	12,4
T. obliquilobum	210	5	2,3
T. jaervikylense	91	2	2,2
T. pulcherrimum	240	31	11,5
T. 1930:722 (Spectabilia)	186	1	0,6

In *Hieracium*, BERGMAN was able to ascertain that occasional E.M.C:s form tetrads and small nuclei. Mature embryo-sacs with a

reduced number do not seem to occur. I have also observed degenerating cells that originate from a reductional division. In my material it is certain that they do not produce mature embryo-sacs, and at most attain a frequency of 1—2 per cent. Nevertheless the achenes are to a great extent empty or are incapable of germinating. As in the case of *Antennaria* and *Poa* this is no doubt due to the peculiar type of division.

8. PARTHENOGENESIS AND SUPPRESSION OF CROSSING-OVER.

The process by means of which parthenogenetic meiosis acquires its most essential characteristic, viz. the suppressed pairing in the female organs, cannot be compared with the findings of recessive mutations as the cause of the failure of pairing in the male organs. Instead a parallel can be drawn between it and the peculiar maturation divisions in certain animals, where crossing-over fails in one of the sexes.

The circumstances which cause this phenomenon in *Drosophila* have been summarized by GOWEN in 1922. They can be divided into three classes: 1) The well-known condition that crossing-over always fails in the autosome pairs in the male (MORGAN). No single genes have as yet been shown to be responsible for it. 2) Dominant factors reduce crossing-over in the female (STURTEVANT). 3) Recessive factors do not admit of crossing-over in the female. They also effect the chromosomes, of which they do not form part (GOWEN). Later, ANDERSON (1929) was also able to show a gene in the *X*-chromosome which causes sterility in the male and lethality in the female in a homozygous condition. This furthermore brings about reduced — annulled crossing-over in its vicinity and at the same time an increased frequency of non-disjunction. He also succeeded in showing (p. 434) »that the chromosomes which go into exceptional eggs — non-disjunctional — are selected preponderantly from the non-cross-over classes. This virtually means that of the two processes, crossing-over is the first to take place or at least to be determined and secondary non-disjunction is a subsequent process». In other words, the strength of pairing decreases.

Case 1 above, failure of crossing-over in the male, can be due either to failure of zygotene pairing or to the failure of chiasma formation. Failure of crossing-over has been ascertained in a number of animals (DARLINGTON, 1934, p. 110). In *Drosophila pseudo-obscura* ♂, DARLINGTON shows that the autosomes undoubtedly lie in pairs although chiasmata are never formed (in his opinion due to changed

precocity). In *Sciara*, METZ, MOSES and HOPPE (1926, p. 241) discovered that: »in spermatogonial prophases of *Sciara coprophila* however, there is no trace of pairing and the full diploid number is present». A corresponding statement was made by HERTWIG (1920) with regard to the parthenogenetic eggs of *Rhabditis*. Even in the parthenogenetic meiosis in *Taraxacum* and *Hieracium* I have succeeded in ascertaining that primary pairing, if it occurs at all, is very rare.

That a change in precocity is not the cause of the failure of chromosome pairing in the male of *Sciara* (any more than it is the cause of the same phenomenon in the female organs in *Taraxacum*, *Rhabditis*, etc.) is fully demonstrated by the recent investigation of METZ (1931). In somatic cells in *Sciara coprophila* so-called somatic pairing is always present, such as it commonly occurs in other *Diptera. In both spermatocytes and spermatogonia, on the other hand, the chromosomes always remain separated at all stages.* »The contrast in this respect is particularly striking in prophase figures, where in somatic cells the union is very intimate and in germ cells the chromosomes are widely separated from one another» (p. 120). Neither lack of homology, nor change in precocity (in somatic cells there is association in the four-threaded stage) can therefore be the cause of this condition. There is no reversion to or identity with somatic mitosis. *It must be assumed that in some way or other a change in the nuclear plasm or in the chromosomes has been brought about so that no attraction can take place.*

As mentioned above, no solitary genes have ever been observed, which are responsible for the difference in linkage between the two sexes in *Drosophila*. The »complete linkage» in the male is not due either to the presence of the *Y*-chromosome, for in *XXY*-females an exchange takes place between the *X*-chromosomes. Nor is it due to the ratio $X : Y$, for exchange takes place also in *XXYY*-females (STERN, 1933). — Does the ultimate cause also here lie in a change in the physiological nuclear conditions? Is suspended pairing in parthenogenetic animals and plants and in heterogametic animals thus conditioned by the same phenomenon: a physiological alteration in the germ-cell producing organs so that the attraction in the two-threaded stage, the fundamental condition of crossing-over, formation of gemini and regular metaphase, disappears?

The literature on this subject thus shows that there is a certain agreement between the failure of pairing in the parthenogenetic apomicts and the males of certain animals. That solitary recessive

genes can cause the failure of primary pairing in parthenogenetic species can hardly be disputed, all discoveries made so far indicate, however, in this case a varying formation of gemini as a result.

9. PARTHENOGENESIS AND PRECOCITY.

In a certain sense DARLINGTON's precocity theory is true, for as far as our present knowledge goes the chromosomes at meiotic prophase are always single (v. also BELLING, 1933; cf. p. 78 concerning *Fritillaria*). But when DARLINGTON states (1932, p. 307) that the essential difference between meiosis and mitosis is »the curtailed resting stage or earlier prophase» he is guilty — in my opinion — of drawing a false inference. Undoubtedly there are cases where the resting stage before meiosis is of short duration (DARLINGTON, p. 301); further the temporary heterotypic character of prophase in the progeny of the sporogenous cells in *Alchemilla* (not the cells themselves) may be evidence of the same thing. In general, however, there is no essential difference between the long duration of the premeiotic and the mitotic stages. If we bear in mind that in plants (*Taraxacum* and *Hieracium* investigated here) the last premeiotic division in the P.M.C:s is terminated by a resting stage during which the P.M.C:s, their nuclei and also the male organs themselves grow vigorously, then the short duration of the resting stage can hardly be the cause of the failure of the chromosomes to divide. This is evidenced by the following cases:

1) Since the parthenogenetic processes aim at a development of embryo vegetatively without the agency of fertilisation one might expect to find in apomictic species a substitution of the meiotic nuclear division by a mitotic division. One expects what is shown by the following scheme:

Mitotically propagating organisms ↘
Mitotically parthenogen. organisms ↙ sexual organisms with meiosis.

In the higher plants (as in all parthenogenetic apomictic species) it was therefore only necessary to drop the »acquired» precocity to enable the »mitotising» to be complete (GUSTAFSSON, 1935). An examination of the conditions of the female organs will show that *neither among animals nor plants do there occur any division that may be called mitotic.* In only one respect (the »*Hieracium*-type» excluded) does it differ from the normal sexual meiosis, viz. in the failure of the primary pairing. Since zygotene pairing occurs in several cases, the failure of

pairing is here not due to any lack of attraction at prophase but only to suspended chiasma formation. In other cases (probably the majority) the single chromosome threads are not attracted to each other, but this cannot possibly be due to the »mitotising» of meiosis, being caused rather by physiological factors (as is shown by the varying rate of pairing in *T. praestans* ♂). All other indications of meiosis are present: the singleness of the leptotene threads (found with some degree of certainty in *Taraxacum* ♀), *chromosome contraction* as pronounced as in sexual species, and finally, the probable occurrence of terminal affinity at metaphase. The last-mentioned feature never occurs at mitosis. *No case of true mitosis in the female organs is known.* With the postulated simple difference between meiosis and mitosis this is incomprehensible.

2) The recorded cases of a short premeiotic resting stage in animals is counterbalanced by the peculiar meiosis in *Hieracium* (also in *Antennaria* and *Eupatorium*). *In spite of the abnormally long resting stage pseudo-homotypic prophases with chromosomes having a heterotypic appearance are formed and also metaphases with highly contracted chromosomes.* After a still longer delay and a more vigorous growth prophases with mitotic-like chromosomes are, however, occasionally formed. Still there is no justification to conclude that the division in its entirety is synonymous with a somatic mitosis merely on account of the appearance of the metaphase chromosomes.

The most noteworthy and significant evidence against the precocity theory is the occurrence of the pseudo-homotypic metaphase even in those cases in which the duration of the resting stage has been increased. There is therefore no evidence in favour of the precocity theory in *Hieracium*, as BERGMAN considers, quite the contrary.

3) It would appear as if ROSENBERG's classic study of pollen degeneration in *Hieracium* also supplies a series of phenomena showing the substitution of meiotic division by a mitotic. Only in the most important point do these degenerative phenomena differ from mitosis, they do not attain a somatic longitudinal division direct (GUSTAFSSON, 1935). ROSENBERG himself calls attention to this (1927, p. 330): »Die Tatsache, dass hier auch ein Kontraktionsstadium auftritt, deutet darauf hin, dass die P.M.Z.-Teilung doch nicht ganz einer somatischen Teilung gleichgestellt werden kann, sondern richtiger als ein Grenzfall des Übergreifens der homöotypischen Teilung aufzufassen ist».

4) »The mitotised divisions» in *Hieracium* ♂ are not correlated with any protracted resting stage. ROSENBERG (1927, p. 318, cited also

by DARLINGTON, 1932, p. 348) and later BERGMAN consider that the division instead sets in earlier than in the sexual species.

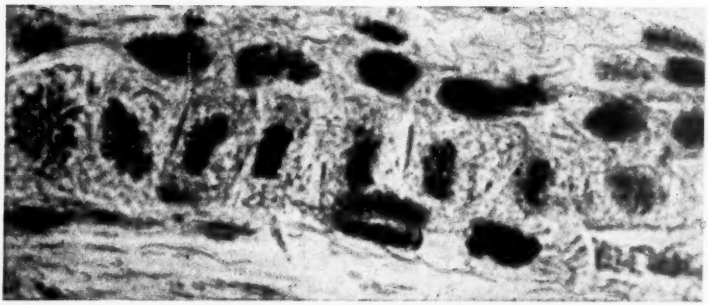
5) Only in one *Hieracium* apomict, *H. lapponicum*, has there been observed an indubitable case of somatic mitosis in the P.M.C:s instead of meiosis. Contraction stages before that are not found. The prophases have the mitotic spireme-like appearance, and the metaphase chromosomes are not contracted as in a meiosis. *No unusual increase in the size of the nucleus and cell takes place, nor is the duration of the resting stage increased to any noticeable degree.* The P.M.C:s lie — as in ROSENBERG's and BERGMAN's cases — close to each other and are not rounded. Thus there is no parallelism with the long duration of the resting stage in the female organs. An interesting point in this connection is that anaphases never occur and that the nuclei degenerate after metaphase.

6) The male meiosis in *Sciara coprophila* (p. 99).

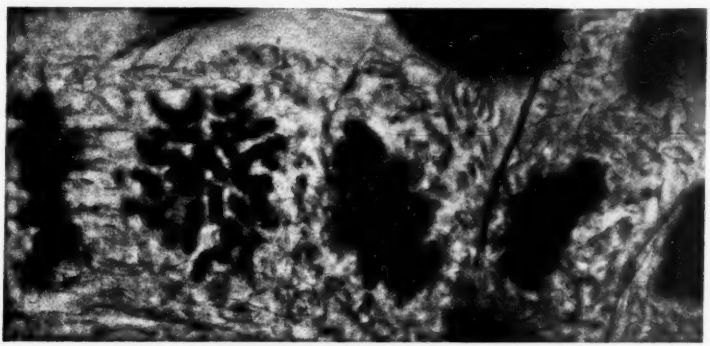
We thus see that there is only one case within the whole of the plant kingdom in which meiosis in the sexual organs has been substituted by a typical mitosis and in this case there is no indication of a resting stage protracted beyond the normal period. Since the changed precocity found so far in sexual species effects only solitary chromosomes or parts of them (localized chiasmata), while the character of the divisions has never been altered, on the whole no evidence can be produced in proof of the precocity theory as it has been set forth by DARLINGTON. His assertion of »the curtailed resting stage or earlier prophase» is purely hypothetical and is probably wrong. DARLINGTON places, one might say, the resting stage as a kind of loose box on the chromosomes, and in his view it can be shortened or lengthened independently of the chromosomes. According to the precocity theory, meiosis ought to be able to appear in organs with many divisions rapidly succeeding each other!

The difference between meiosis and mitosis, which DARLINGTON and BELLING (1933) have emphasized, nevertheless remains. The chromosomes are probably divided in the resting stage of mitosis but in the course of the prophase at meiosis. If this condition is not due to the varying duration of the resting stage, then the chromosomes themselves must be responsible for the occurrence or failure of their division. *In the mitotic, but not in the meiotic, resting stage the chromomeres (the genes) and the chromosome threads reproduce themselves.*

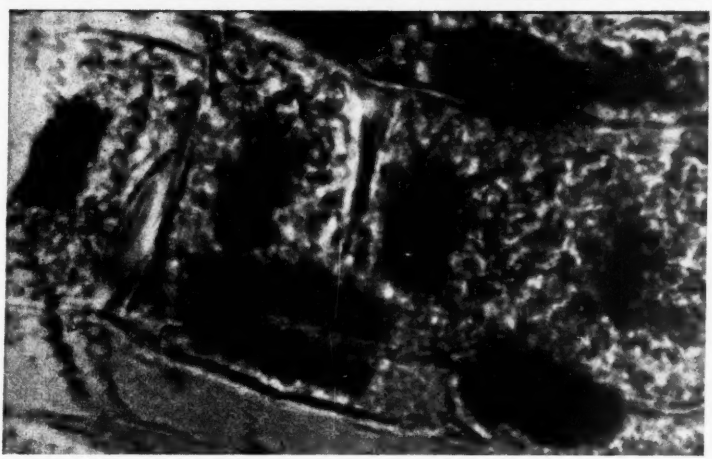
If one attributes the difference between meiosis and mitosis to



167 a



167 b



167 c

Fig. 167. *H. lapponicum* Fr. The degeneration of the somatic division in P.M.C:s. To the left of *a* and *b* a somatic metaphase in polar view, then stages with gradually increasing hydration of the chromosomes (mostly side views). — *a*, 1300 ×, *b*—*c*, 2400 ×. Photo O. Mattsson.

this simple condition one avoids, as DARLINGTON does, making the long or short duration of the resting stage independent of the chromosomes themselves. *For it is probable that the duration of the resting stage is determined by the chromosomes.* When their dehydration has reached a certain point, they absorb pigment and become »differentiated» from the surrounding nuclear sap. Then the so-called resting stage comes to an end. Parthenogenesis in *Hieracium* constitutes a proof of this. *The intense hydration here causes a longer resting stage.*

What DARLINGTON has called differential precocity, that is to say, the early division and condensation of solitary chromosomes (often the sex chromosomes), is a specific property of the chromosome or pair of chromosomes in question. »The general character of this behaviour makes it clear that we are dealing with a reaction of particular chromosomes to special genetic conditions rather than with the reaction of dissimilar homologues with one another in pairing such as is characteristic of structural hybrids» (DARLINGTON, p. 349). In these cases the duration of the resting stage has no significance whatever.

This reproduction theory offers no explanation either as to *why* meiosis, when it has arisen, makes chromosomes and resting stage dependent on each other. The chromosomes determine the duration of the resting stage but the division and condensation of the chromosomes are caused by physiological causes in the nucleus and plasm, of which we know nothing. To a certain degree division and contraction may also vary in different pairs of chromosomes (sex chromosomes or autosomes).

HUSKINS and SMITH (1934) have to a certain extent criticized the precocity theory along the same line. They have based their arguments, however, on the probably erroneous view that the chromosomes in ordinary mitosis divide already at a stage prior to the resting stage. In their opinion, the difference between meiosis and mitosis is therefore due to a retarded division of the meiotic chromosomes rather than to a precocious start of the prophase.

The same causes that bring about the periodic development of organs for the formation of sex cells *should lead to the failure of the chromosomes to reproduce themselves and thereby to the setting in of meiosis.* The failure of reproduction thus results in the occurrence of the primary pairing at prophase, but is itself caused by external physiological factors. Sexual organs are formed, *hence* meiosis must take place. This explains the curious phenomenon that parthenogenetic meiosis in the female organs has never been able to turn into

mitosis. Thus, we arrive at the conclusion that mitosis and meiosis have become widely differentiated in higher organisms during the phylogenetic development, and that, therefore, the reversion from meiosis back to mitosis is not easily accomplished.

SUMMARY.

1) The male and female meiosis of various *Taraxacum*, *Archieracium*, *Erigeron* and *Marsilia* biotypes have been examined.

2) The classification of parthenogenesis among plants into the *Alchemilla*, *Taraxacum* and *Antennaria* schemes is rejected.

3) The zygoid parthenogenesis is thought to consist of three processes: a) The primary pairing is decreased or omitted, b) the zygoid chromosome numbers arise through restitution nuclei, pseudo-homotypic metaphases and so-called somatic divisions, c) the egg-cell develops without any fusion of nuclei and cells.

4) The cause of the failure of primary pairing is probably identical with the cause of the failure of pairing and crossing-over in many heterogametic animals (*Sciara*, *Drosophila* males).

5) The origin of restitution nuclei is correlated with the univalence of the chromosomes but not caused by it. The restitution nuclei in the E.M.C:s of *Taraxacum* is formed at the periphery of the spindle, at the same time as or shortly after the spindle stretches. In the P.M.C:s the shape of the restitution nuclei is irregular. Probably they arise within the spindles at different distances from the periphery.

6) A pseudo-homotypic metaphase arises, when the stretching of the spindle is omitted and the univalents gather in the equator to divide.

7) The so-called somatic division is probably nothing but a degeneration phenomenon (an ageing of the cell) and is accompanied by certain cytological peculiarities, a high frequency of empty fruits and a low germination power of the developed seeds.

8) It is shown that the precocity theory does not apply to the parthenogenetic phenomena.

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CONTENTS.

I. Special Part 1
1. The Nomenclature of the Apomictic Phenomena 1
2. Material and Methods 3
3. The Cytology of *Taraxacum* and Female *Archieracium* 6
A. Previous Investigations of the Development of the Macrospores in *Taraxacum* 6
B. *Taraxacum* 9
C. *Archieracium* 38
4. The Development of Seed in *Hieracium* and *Taraxacum* 45
5. The Male Division in *H. lapponicum* 51
6. *Erigeron* 54
7. The Zygoid Parthenogenesis in the Cryptogamia 56
II. General Part 58
1. The Male Meiosis in *Taraxacum* and the Hybrid Hypothesis 58
2. Chromosome Number and Apomixis 61
3. The Automictic Parthenogenesis among Animals 63
4. Wall-formation as a Principle of Classification in the Parthenogenetic Phanerogams 65
5. The so-called *Alchemilla* Scheme 69
6. The Mechanism of Zygoid Parthenogenesis 73
A. The Failure of Bivalent Formation in the Female Organs 74
B. The Formation of Zygoid Chromosome Numbers 79
a. The Formation of Restitution Nuclei and its Causes 83
b. The Mechanism of the Pseudo-homotypic Division 89
c. The so-called Somatic Division in the Female Organs 91
C. The Development of the Parthenogenetic Egg-cell 93
7. Stabilized and Unstabilized Parthenogenesis 95
8. Parthenogenesis and Suppression of Crossing-over 98
9. Parthenogenesis and Precocity 100
Summary 105
Literature cited 106

A SECONDARY MUTATION FROM WHITE TO A DARKER ALLELOMORPH IN DROSOPHILA MELANOGASTER

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MANY spontaneous mutations have occurred at the white-eye locus in *Drosophila*, producing the well known series of multiple allelomorphs, ranging in color from the red of the wild type eye through coral (w^{co}), blood (w^{bl}), eosin (w^{e}), cherry (w^{ch}), apricot (w^{a}), buff (w^{bf}), tinged (w^{t}), ivory (w^{i}), and ecru (w^{ec}) to white (w). Nearly all of these have arisen by mutation of a wild type gene to a recessive allelomorph. Rarely one of these mutant allelomorphs has again mutated, for example eosin has on several occasions mutated to white. Such secondary mutations which result in a further departure from wild type have been called by MOHR (1922) progressive mutations. Secondary mutations in the contrary direction from mutant allelomorphs to or toward wild type are much rarer. The majority of these are complete reverse mutations from mutant to wild type at one step. The rarest mutation of all is from a mutant to another allelomorph which represents only a partial return to the wild type characters. This has been called *regressive* mutation and is only known to have occurred once spontaneously at the white locus, viz., the original mutation of eosin from white as reported by MORGAN and BRIDGES (1916). It is of interest therefore to record the origin of a new allelomorph of white which can be shown to have arisen not from wild type but by regressive mutation from white, and which provides a useful new member of this series of allelomorphs.

The new mutant was found as a single male among the progeny of the culture described below:

TABLE 1. *Culture C 23 (10/27/34).*

♀ w/w; L^{sl^h}/Cy × ♂ b pr vg^{no} L

♀ L/Cy	♀ L	♂ w; L/Cy	♂ w; L	♂ w^{s}; L/Cy !
64	45	60	48	1

The exceptional male had yellowish-brown eyes of about the color of honey, darker and yellower than buff, a little lighter and less

orange than apricot. From its appearance and manner of origin it was judged to be an allelomorph of white and was therefore crossed to white, wild type and cherry (w^{ch}) females with the following results:

TABLE 2. *Culture C 88 b.*

♀ white (w/w; Cy) × ♂ »honey» (w^x; L/Cy)

Cy ♀	L/Cy ♀	L ♀	♂	♂	♂
light honey	light honey	light honey	w; Cy	w; L/Cy	w; L
15	18	24	21	14	12

All daughters were intermediate in color between the new mutant color and white. All sons were white.

TABLE 3.

♀ cherry $\frac{w^{ch}}{w^{ch}}$ × ♂ w^x; L/Cy »honey»

	♀	♀	♂	♂
	light cherry	light cherry	cherry	cherry
C88c	Cy	L	Cy	L
	59	69	73	15

All daughters were intermediate in color between cherry and the new mutant color. All sons were cherry.

A mating of the mutant male to wild type (C 88 d) gave only wild type eye color in sons and daughters: 65 Cy (36 ♀ 29 ♂), 68 Lobe (43 ♀ 25 ♂).

These results show clearly that the mutant male contained a recessive gene allelomorphic with white. This has been called honey (w^h). His composition was thus w^h; L/Cy and the mutation must have occurred in the X-chromosome of his white mother, i. e. $w \rightarrow w^h$. The presence of other genes excludes the possibility of origin from any other culture. The mother of the mutant was from an inbred stock of white containing also a Lobe allelomorph (L^x, possibly the same as L^2 of other workers), a II chromosome lethal l^h, balanced over Curly. This stock had been under continuous observation for two years and had produced no other mutants. The original source of the white gene of this stock is unknown.

A homozygous stock of the new mutant was subsequently extracted from the cross to wild type and freed from other mutant genes. The colors of its compounds with white, apricot, cherry and Notch 8

(a deficiency for the white locus) were compared with the homozygous types in the same cultures.

Observations of the pure honey stock showed that the eye color of the male is clear light brownish yellow, with a slightly lighter »halo» at the edge of the eye. It most nearly resembles the apricot mutant (w^a) but differs from it in being slightly lighter and in having no orange or pinkish tinge. The eyes of the female are slightly but distinctly darker than those of the male with less halo and a slight orange tinge, whereas in all three of the apricot allelomorphs, the males have lighter eyes than the females (BRIDGES, personal communication). In the same culture newly hatched honey flies can be easily separated from apricot and from cherry. The eyes of the honey flies darken slightly and very slowly with age, whereas apricot and cherry darken more quickly, so that the differences between honey and both of the other mutants increase with age.

The following combinations have been observed under comparable conditions of age and culture and are arranged in decreasing order of darkness

$$\begin{array}{ll} ♀♀ & w^{ch}/w^{ch} \rangle \begin{cases} w^{ch}/w \\ w^{ch}/w^{h} \end{cases} ? \, w^a/w^a \rangle w^a/w^h \rangle w^h/w^h \rangle w^a/w \rangle w^a/N^{s} \rangle w^h/w \rangle w^h/N^{s} \rangle w/w \\ ♂♂ & w^{ch} \rangle\rangle \, w^a \rangle \, w^h \rangle\rangle \, w \end{array}$$

The order of the allelomorphs studied is very clearly in order of decreasing darkness cherry, apricot, honey, white. The greatest differences are those between cherry and apricot and between honey and white. Honey female is only slightly lighter than apricot female. The same order is found in the compounds of honey: $w^h/w^{ch} \rangle w^h/w^a \rangle w^h/w^h \rangle w^h/w$. Here in addition it is clear that the compound with cherry is pinkish, while that with apricot has more orange tinge than honey.

Among the other compounds the relative order of w^a/w^a and w^{ch}/w^h is not clear since these have not been compared in the same culture. w^{ch}/w^h is probably the darker. The most difficult classifications are those involving separation of w^a/w^a, w^a/w^h, w^h/w^h and w^a/w, although our ratios show that after practice these classes can be separated.

One unexpected fact was observed in the inability to separate w^{ch}/w^h from w^c/w. These classes were nearly alike in color indicating a similar diluting effect of w and w^h on cherry, although the w^a/w^h and w^a/w compounds were separable.

In view of MOHR's (1923) discovery that a deficiency for the white

locus (Notch 8) has a greater diluting effect on the allelomorphs blood, coral, eosin, apricot and buff than the white gene itself, tests were made to determine whether Notch 8 has a similar effect on honey and whether this would serve further to distinguish w^h and w^a.

Honey and apricot males were crossed with Notch 8 females and with white females. From the Notch crosses the Notch females showed the mutant eye colors and these were compared with the respective compounds with white.

w^a/N^8 was much darker than w^h/N^8 and had distinctly more orange tinge. The N^8 compound was in each case *lighter* than the corresponding white compound, as follows: $w^a/w \rangle w^a/N^8 \rangle w^h/w \rangle w^h/N^8$. w^a/N^8 was only slightly darker than w^h/w and separation was not certain. w^h/N^8 was pale yellow, slightly but distinctly lighter than w^h/w. Thus the diluting effect of Notch 8 serves further to confirm the distinctness of the new mutant from apricot which it most nearly resembles. I have had no opportunity to compare honey with buff, but from the descriptions of SAFIR (1916) and MORGAN, BRIDGES and STURTEVANT (1925) buff is apparently much lighter in color, shows little or no sex-dimorphism, and has a pinkish tinge which honey lacks entirely [1].

DISCUSSION.

From the above facts it can be concluded that honey is a new and different allelomorph of white which arose by spontaneous regressive mutation of a white gene. The reversibility of mutation has already been proved by the occurrence of spontaneous reverse mutations at this locus (eosin) and at others, although it remains a very rare occurrence except in the cases of very mutable genes such as those studied by DEMEREC (1928). Reverse mutations have been induced by irradiation in the case of the forked and scute loci by PATTERSON and MULLER (1930) and at the white locus by TIMOFÉEFF-RESSOVSKY (1928—33). LOBASOV and SMIRNOV (1934) report a mutation of eosin to a darker allelomorph following treatment with ammonia, while JOLLOS (1935) has reported two cases of complete reversion of eosin and of white to wild type, although he gives no supporting evidence. The extensive experiments of JOHNSTON and WINCHESTER (1934) have

[1] From a cross of $N^8/lz \triangle 49 \times w^h$ one exceptional honey son was found. This was tested and found to be sterile and so was probably XO from non-disjunction. The eye color was that of a normal honey male so that the sex dimorphism in honey eye color is probably not due to the Y-chromosome.

shown that irradiation induces reverse mutations with much lower frequency than mutations from wild type allelomorphs, and they found no reverse mutations at all at the white locus (w^a gene treated). Regressive mutation at the white locus is thus very rare indeed, although the evidence from the present case leaves no doubt that it does occur spontaneously.

In addition to providing a new useful allelomorph for marking the white locus, honey adds a new step in the remarkable series of eye color changes already reported at this locus. The order of effect of the genes of this series as summarized by MORGAN, BRIDGES and SCHULTZ (1931) and with the new allelomorph inserted is as follows:

Colors	coral	blood		eosin	cherry	apricot	honey	buff	tinged	ivory	white
Alleles	w^{co}	w^{bl}	w^{30}	w^{e}	w^{ch}	w^{a}	w^{h}	w^{bf}	w^{t}	w^{i}	w
Sex diff.:	♂〉♀	♂〉♀	♀〉〉♂	♀〉〉♂	♀〉〉♂	♂〉♀	♀〉♂	♀〉♂	?	♀〉♂	♀ = ♂

Symbols: 〉 darker, 〉〉 much darker, 〉 slightly darker.

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KONSTANZ DES CHLOROPHYLLGEHALTES UND CHROMATOPHORENDEGENERATION CHLOROPHYLLMUTIERENDER GERSTEN-SIPPEN

VON *H. v. EULER, B. BERGMAN, H. HELLSTRÖM und D. BURSTRÖM*

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VOR etwa zwei Jahren untersuchten wir (v. EULER, BURSTRÖM und HELLSTRÖM, 1933) die Konstanz des Chlorophyllgehaltes bei verschiedenen Gerstensorten und davon herstammenden Heterozygoten, nämlich

die Westergaard-Linie,
eine Svalöf-Gerste, Sval Xa, und
Probsteier-Gerste.

In dieser und unseren folgenden chemisch-genetischen Mitteilungen werden wir im Einverständnis mit Herrn Prof. NILSSON-EHLE die nachstehenden abgekürzten Bezeichnungen für die untersuchten Sippen und Linien verwenden:

W = Westergaards Linie, homozygot. Ihr Heterozygot W het alb 1 spaltet im Verhältnis 1 W : 2 W het alb 1 : 1 Albina 1.

Sval alb = vierzeilige Svalöfsorte, homozygot. Ihr Heterozygot Sval alb het alb 2 spaltet im Verhältnis 1 Sval alb : 2 Sval alb het alb 2 : 1 Albina 2.

Go × Chev = Linie aus Kreuzung Goldgerste × Chevalier de Garton. Ihr Heterozygot Go × Chev het alb 3 spaltet im Verhältnis 1 Go × Chev : 2 Go × Chev het alb 3 : 1 Albina 3.

Prob = Probsteier-Gerste, homozygot. Ihr Heterozygot Prob het Xa 2 spaltet im Verhältnis 1 Prob : 2 Prob het Xa 2 : 1 Xantha 2.

Sval Xa = vierzeilige Svalöfsorte, homozygot. Ihr Heterozygot Sval Xa het Xa 1 spaltet im Verhältnis 1 Sval Xa : 2 Sval Xa het Xa 1 : 1 Xantha 1.

In einer weiteren Mitteilung (v. EULER und BERGMAN, 1933) wurde festgestellt, dass bei den untersuchten Formen die Chromatophoren von Albina stark degeneriert sind, dass die Chromatophoren der chlorophylldefekten Mutanten Xantha 1 und Xantha 2 nur wenig ver-

ändert sind, sodass man kaum von einer Degeneration sprechen kann, und dass

die Chromatophoren von Alboxantha von denen der Albina und der Xantha abweichen, und zwar sowohl durch ihre geringe Anzahl als durch ihre Grösse.

Bei Albina 1, 2, 3 und 7, welche nur wenige Wochen lebensfähig sind, ist also die Anormalität der Chromatophoren augenscheinlich.

In Zusammenhang mit diesem Befund steht dann unser Resultat, dass die mittlere Chlorophyllkonzentration in Xantha 1 im Mittel $^1/_3$ der normalen Chlorophyllkonzentration beträgt. Der Chloroplast ist hier auch in den Mutanten vorhanden — ob ganz oder nur teilweise wissen wir noch nicht — und es kann sich hier um den Aufbau des Chlorophylls selbst handeln, während bei Albina die Synthese oder die Vermehrung des Chloroplasten selbst gehemmt zu sein scheint; demgemäss fehlt in Albina auch Carotin und Xanthophyll.

Da wir versuchen, an dem von Prof. NILSSON-EHLE gelieferten Material die chemische Entwicklungsreihe des Chlorophylls festzustellen, schien es uns notwendig, die Konstanz der mutierenden Eigenschaft, nämlich der Chlorophyllkonzentration festzulegen. Wir hatten deshalb viele Individuen auf ihren Chlorophyllgehalt untersucht und haben die Einzelbestimmungen in Kurven zusammengestellt.

Derartige Kurven — Verteilungskurven — über eine gewisse Eigenschaft einer Sippe sind früher von W. JOHANNSEN (1926) eingehend studiert und diskutiert worden.

An einer chemisch definierten Eigenschaft, besonders am Chlorophyllgehalt, war bis jetzt unseres Wissens die Konstanz bzw. die Variationsbreite zum ersten Mal in unserer früheren Arbeit untersucht worden.

Seitdem haben wir (v. EULER, BERGMAN und HELLSTRÖM, 1934) auch das Verhältnis zwischen der Anzahl der Chloroplasten und dem Chlorophyllgehalt von Blättern an einem besonderen Material, nämlich *Elodea densa* untersucht. Wir fanden, dass das Chlorophyll in Chloroplasten nur etwa 6 % des Gewichtes ausmacht und haben geschlossen, dass in Chloroplasten pro Molekül Chlorophyll höchstens *eine* und zwar ca. 10—20 Mal so grosse ligatorische Gruppe vorhanden sein kann.

Wir haben nun an zwei uns von Prof. H. NILSSON-EHLE übergebenen Röntgengoldgersten in ähnlicher Weise wie früher an Goldgerste und an der Sorten Sval Xa und Prob und ihren Heterozygoten viele

einzelne Individuen auf ihren Chlorophyllgehalt hin untersucht und eine Variationskurve für beide Röntgengoldgersten festgelegt. Wir geben die Resultate dieser Untersuchung in folgenden Tabellen an.

INDIVIDUELLE CHLOROPHYLLVERTEILUNG IN DEN LAUBBLÄTTERN VON RÖNTGENGOLDGERSTE I, 1934—244 UND RÖNTGENGOLDGERSTE II, 1934—240 (NILSSON-EHLE).

a) *Röntgengoldgerste I (1934—244).* — Spaltet in 75 % grün und 25 % weiss.

TABELLE 1.

Nr.	$\frac{1}{g} \cdot \log \frac{Io}{I}$	Mittelwert	Δ	Nr.	$\frac{1}{g} \cdot \log \frac{Io}{I}$	Mittelwert	Δ	Nr.	$\frac{1}{g} \cdot \log \frac{Io}{I}$	Mittelwert	Δ
1	3,39		+ 0,10	26	3,87		— 0,18	51	5,08		+ 0,73
2	2,84		— 45	27	3,84		— 21	52	4,10		— 25
3	3,36		+ 07	28	3,95		— 10	53	4,56		+ 21
4	3,98		+ 69	29	3,60	4,05	— 45	54	3,41		— 94
5	3,16		— 13	30	4,45		+ 22	55	4,16	4,35	— 19
6	3,65		+ 36	31	4,43		+ 20	56	4,49		— 05
7	2,93		— 36	32	3,81		— 42	57	4,40		— 14
8	3,12		— 17	33	4,39		+ 16	58	4,41		— 13
9	3,18	3,29	— 11	34	3,37		— 86	59	4,08		— 46
10	4,14		+ 30	35	3,75		— 48	60	4,88		+ 34
11	3,33		— 51	36	4,52		+ 29	61	4,91		+ 37
12	3,48		— 36	37	4,10		— 13	62	4,81		+ 27
13	4,04		+ 20	38	4,43		+ 20	63	4,73		+ 19
14	3,79		— 05	39	4,53		+ 30	64	4,62		+ 08
15	4,36		+ 52	40	3,75		— 48	65	3,73		— 81
16	3,73		— 11	41	5,00		+ 77	66	4,95		+ 41
17	4,00		+ 16	42	4,50	4,23	+ 27	67	4,90		+ 36
18	3,83		— 01	43	3,69		— 66	68	4,14	4,54	— 40
19	3,74	3,84	— 10	44	4,68		+ 33	69	3,23		— 73
20	3,86		— 19	45	4,50		+ 15	70	4,81		+ 85
21	4,38		+ 33	46	5,00		+ 65	71	3,96		± 00
22	4,20		+ 15	47	4,56		+ 21	72	3,21		-- 75
23	4,04		— 01	48	3,58		— 77	73	4,35		+ 39
24	4,18		+ 13	49	5,00		+ 65	74	4,18	3,96	+ 22
25	4,55		+ 50	50	4,18		— 17				

Die Querstriche geben die Grenzen zwischen den verschiedenen Ähren an. Die Mittelwerte sind für jede Ähre berechnet worden.

Etwa 100 Körner aus 7 Ähren wurden in Wasser eingeweicht, ährenweise in je dem gleichen Blechkasten auf Filtrierpapier ausgesät. Sobald das Laubblatt sich zu entwickeln beginnt, wurden die Pflanzen 7 Tage lang dem Tageslicht ausgesetzt. Da diese Untersuchung im Dezember in Stockholm ausgeführt wurde, war die Belichtung gering und die Pflanzen machten deshalb einen bleichen und etiolierten Eindruck.

Zur Bestimmung wurde nur das erste Laubblatt verwendet, welches gemessen, gewogen, in kleine Teile zerschnitten und mit Alkohol bis zu einem Volumen von 10 ccm extrahiert wurde. In den so gewonnenen Extrakten wurden die Chlorophyllmengen bei $\lambda = 668\ m\mu$ lichtelektrisch bestimmt. Die einzelnen Ergebnisse sind in den Tabellen 1—5 zusammengefasst.

TABELLE 2.

Intervall	−119 bis − 90	−89 bis −60	−59 bis −30	−29 bis 0	1 bis 30	31 bis 60	61 bis 90
Anzahl Abweichungen	1	7	9	20	20	11	6

Zur näheren Charakterisierung der Kurve sind aus derselben die folgenden Werte berechnet worden.

$$s = \text{Standardabweichung} = \pm\sqrt{\frac{\Sigma\Delta^2}{n}}$$

$$S = \text{Schiefheit} = \frac{\Sigma\Delta^3}{n} : s^3$$

$$E = \text{Exzess} = \left[\frac{\Sigma\Delta^4}{n} : s^4\right] - 3$$

Für diese Ausdrücke wurden folgende Zahlen gefunden:

s	S	E
0,41	−0,25	−0,43

S, die Schiefe, ist negativ aber so klein, dass dieselbe keine Rolle spielt. E, der Exzess, hat ebenfalls einen negativen Wert, −0,43. Derselbe ist hinreichend gross, um deutlich zu zeigen, dass der höchste Punkt der »Treppenkurve» niedriger liegt als derjenige der idealen Kurve. Der Exzess ist indessen zu klein, als dass zwei höchste Punkte angenommen werden könnten. Mittelwert = 4,04, entsprechend 0,27 mg Chlorophyll per g Frischgewicht.

b) *Röntgengoldgerste II (1934—240).* — Spaltung gefunden in 75 % grün und 25 % gelbgrün.

1 Pflanze, ca. 100 Körner, enthaltend 5 Ähren, wurde ährenweise

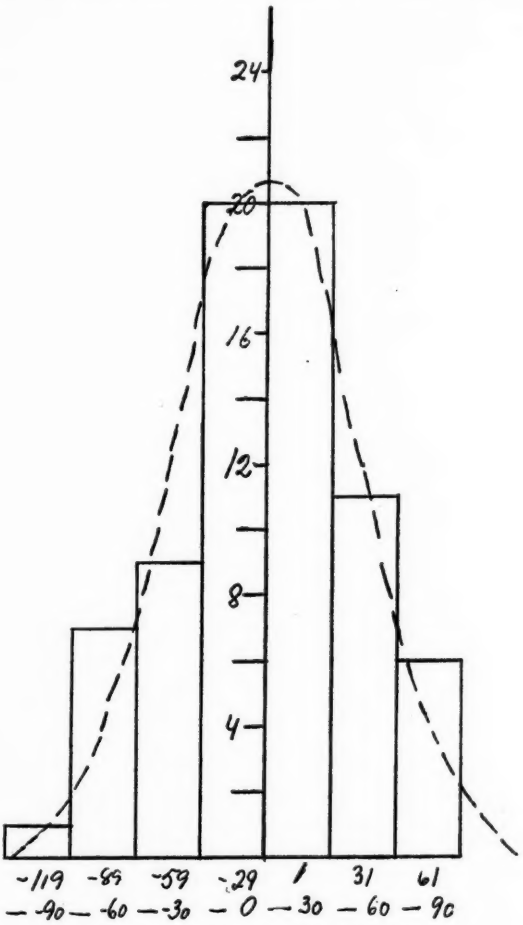

Fig. 1. (— — — = Ideale Kurve).

in einem Blechkasten gesät. Tageslichtbelichtung 9 Tage lang. Die Methodik war die gleiche wie für Röntgengoldgerste I.

Tabelle 3 zeigt, dass die Chlorophyllmenge im Anfang zunimmt, ein Maximum erreicht, und dann wieder abnimmt. Dies

TABELLE 3.

Nr.	$\frac{1}{g} \cdot \log \frac{Io}{I}$	Mittelwert	Δ	Nr.	$\frac{1}{g} \cdot \log \frac{Io}{I}$	Mittelwert	Δ	Nr.	$\frac{1}{g} \cdot \log \frac{Io}{I}$	Mittelwert	Δ
1	3,97		— 0,94	34	5,37		— 0,22	62	5,49		— 0,31
2	4,44		— 47	35	6,57		+ 98	63	6,11		+ 31
3	4,72		— 19	36	5,38		— 21	64	5,80		± 00
4	4,53		— 38	37	5,40	5,59	— 19	66	5,33		— 47
5	5,28		+ 37	38	5,43		— 19	67	5,96		+ 16
6	4,84		— 07	39	6,23		+ 61	68	6,04		+ 24
8	5,95		+ 1,04	40	5,09		— 53	69	6,02		+ 22
9	5,93		+ 1,02	41	4,84		— 78	70	5,64	5,80	— 16
11	5,19		+ 0,28	43	6,21		+ 59	72	5,24		— 49
12	4,21	4,91	— 70	44	6,90		+ 1,28	73	6,02		— 29
13	5,90		+ 50	45	4,63		— 0,99	74	6,39		+ 66
14	5,30		— 10	46	5,95		+ 33	76	5,92		+ 19
15	4,82		— 58	47	6,09		+ 47	77	6,78		+ 1,05
10	4,96		— 44	48	4,87	5,62	— 75	78	5,25		— 0,48
16	4,70		— 70	49	5,47		— 11	79	6,13		+ 0,40
18	7,23		+ 1,83	50	6,44		+ 86	81	4,87		— 86
19	5,11		— 0,29	51	5,87		+ 29	82	5,20		— 53
23	5,93		+ 53	52	5,57		— 01	83	5,51	5,73	— 22
24	4,87		— 53	53	6,27		+ 69	84	4,04		— 1,01
25	5,22	5,40	— 18	54	5,38		— 20	85	6,58		+ 1,53
26	5,28		— 31	55	5,00		— 58	86	4,67		— 0,38
29	5,41		— 18	56	4,10		— 1,48	88	5,14		+ 09
30	4,97		— 62	58	5,90		+ 0,32	89	5,38		+ 33
31	6,92		+ 1,33	59	5,84	5,58	+ 26	93	5,27		+ 22
33	5,15		— 0,44	60	5,37		— 43	96	4,47		— 58
33	5,48		— 11	61	6,22		+ 42	98	4,83	5,05	— 22

dürfte darauf beruhen, dass die Pflanzen durch die Anordnung bei der Keimung ungleich belichtet worden sind, d. h., dass die Pflanzen, welche nahe an den Seiten der Blechkästen gewachsen sind, mehr beschattet wurden als die in der Mitte des Kastens gepflanzten. Bei der Extraktion der Pflanzen sind diese in der Reihenfolge von der einen Seite zu der andern entnommen worden. Bei der Differenzberechnung sind zuerst die allerkleinsten Werte (= 13) entnommen worden (die chlorophylldefekten). Die übrigen, 78 Stück, sind in Gruppen von je 10 Stück eingeteilt worden. Für jede Klasse ist ein Mittelwert berechnet worden, und die Differenz zwischen den einzelnen Bestimmungen und den der Gruppe zugehörende Mittelwert ist als Δ bezeichnet.

TABELLE 4.

Nr.	$\frac{1}{g} \cdot \log \frac{Io}{I}$	Mittelwert	Δ
7	2,37		— 0,48
21	2,30		— 55
22	2,95		+ 10
27	2,43		— 42
28	2,91		+ 06
42	2,65		— 20
65	3,16		+ 31
71	3,27		+ 42
80	3,04		+ 19
87	2,67		— 18
91	3,17		+ 32
92	3,11		+ 26
97	2,97	2,85	+ 12

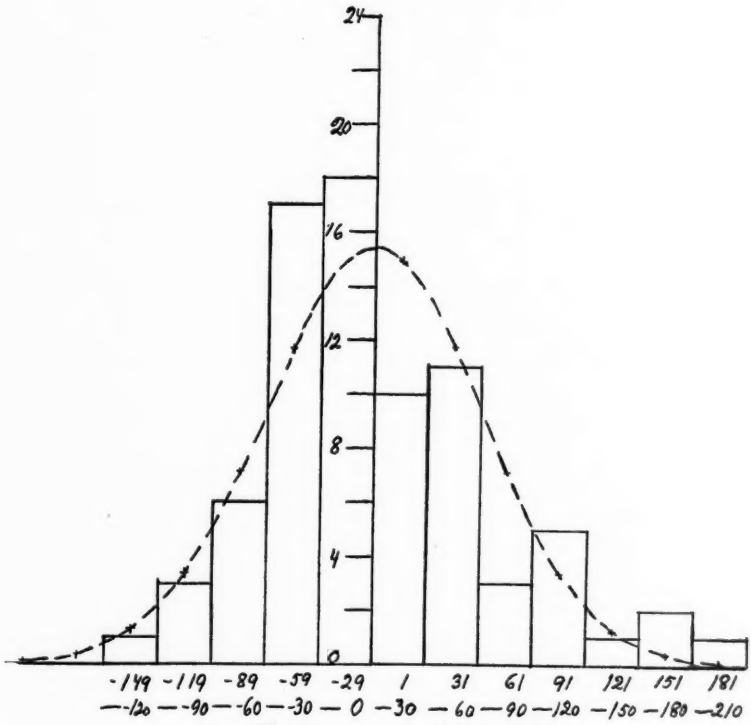

Fig. 2. (— — — = Ideale Kurve).

TABELLE 5.

Intervall	—149 bis —120	—119 bis — 90	—89 bis —60	—59 bis —30	—29 bis 0	1 bis 30	31 bis 60	61 bis 90	91 bis 120	121 bis 150	151 bis 180	181 bis 210
Anzahl Abweichungen	1	3	6	17	18	10	11	3	5	1	2	1

Standardabweichungen s, Schiefe S und Exzess E sind berechnet worden und ergaben folgende Werte:

s	S	E
$\pm 0{,}63$	$0{,}56$	$0{,}24$

Aus diesen Zahlen und der Kurve ergibt sich folgendes:

Die Kurve ist schief und ihre Spitze liegt über derjenigen der idealen Kurve. Der Exzess ist in jedem Fall positiv und klein; es ist ausgeschlossen, dass die Kurve zwei Spitzen besitzt.

Mittelwert = 5,46, entsprechend 0,36 mg Chlorophyll per g Frischgewicht.

Zusammenfassung. — Wie aus den Berechnungen der beiden Versuche und den Figuren 1 und 2 hervorgeht, spricht nichts dagegen, dass die Chlorophyllwerte in den einzelnen Pflanzen innerhalb jeder Reihe die gleichen sind. Ein Unterschied zwischen grünen Homozygoten und grünen Heterozygoten konnte also nicht nachgewiesen werden, was auch schon früher hier hinsichtlich des Chlorophyllgehalts mutierender Pflanzen quantitativ nachgewiesen ist.

MORPHOLOGISCHE UNTERSUCHUNGEN (B. BERGMAN).

Für die morphologische Untersuchung wurde die gleiche Methodik angewandt, wie die, mit welcher früher (v. EULER und BERGMAN, 1933) chlorophylldefekte Gerstenmutanten untersucht worden waren. Die neuen Untersuchungen wurden an fünf Mutanten angestellt. Von denselben zeigten Röntgenmutation I (weiss) und Primus II »gulvit» die stärkste Chromatophorendegeneration[1]. Bei diesen beiden (Fig. 3,1 und Fig. 3,2) sind die Chromatophoren erheblich kleiner und der Form nach sehr unregelmässig im Vergleich mit denjenigen normaler Gerstenpflanzen (Fig. 3,6). Die genannten beiden Mutanten lassen sich ferner viel schwächer färben und die Grenzen dieser Chromatophoren sind nicht so scharf, wie in normalen Fällen. Bei Primus II »gulvit» (Fig. 3,2) kann man oft die »weissen Flecken» beobachten, welche früher für Chromatophoren bei Albina 1 und Albina 7 beschrieben worden sind (l. c.

[1] Die Bezeichnung »gulvit» ist nur vorläufig.

S. 287). Solche weisse Flecken kommen auch bei Röntgenmutation I (weiss) vor, wenn auch viel seltener.

Die starke Chromatophorendegeneration bei Röntgenmutation I (weiss) und Primus II »gulvit» steht in guter Übereinstimmung mit ihrem äusseren Charakter. Die Mutanten der Röntgenmutation I sind somit

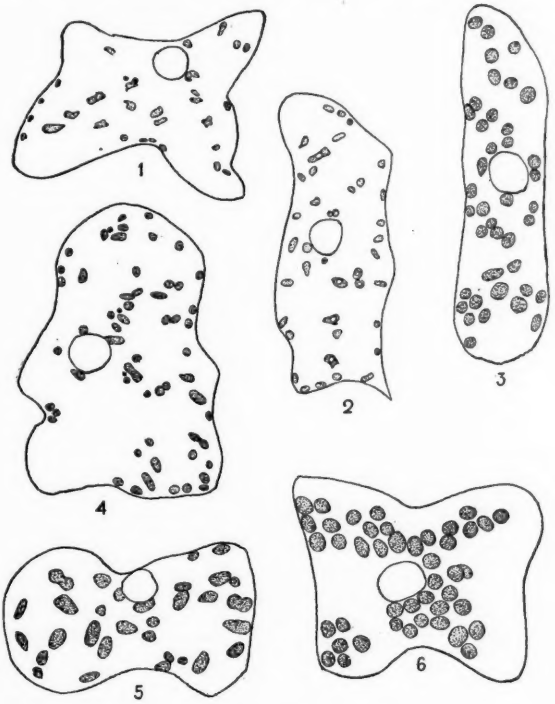

Fig. 3. Mesophyllzellen mit Chromatophoren. — 1. Röntgenmutation I (weiss). — 2. Primus II »gulvit». — 3. Primus II Xanthaurea. — 4. Primus II Xanthalba. — 5. Röntgenmutation II (gelbgrün). — 6. Normale Goldgerste. — (Vergr. 840).

rein weiss; die gulvit-Mutanten von Primus II sind ebenfalls weisslich, aber mit einem geringen Anteil von Gelbfärbung.

Bei den drei übrigen gelbgrünen Mutanten, Primus II Xanthaurea (Fig. 3,3), Primus II Xanthalba (Fig. 3,4) und Röntgenmutation II, gelbgrün (Fig. 3,5), sind die Chromatophoren besser herausdifferentiert. Dies gilt besonders von der ersten und letzten der genannten Mutanten.

Bei Primus II Xanthaurea (Fig. 3,3) stimmen somit die Chromato-

phoren ihrer Grösse und Form nach ziemlich gut mit den normalen Chromatophoren (Fig. 3,6) überein.

Bei Röntgenmutation II (gelbgrün) (Fig. 3,5) ist dagegen, wie die Fig. zeigt, die Form unregelmässiger und die Grösse wechselnd.

Wie bei den zwei letztgenannten sind die Chromatophoren bei Primus II Xanthalba sehr deutlich abgegrenzt und treten gut hervor. Sie sind indessen, wie die Fig. 3,4 zeigt, durchgehend kleiner. Grösse und Form sind, wie bei Röntgenmutation II (gelbgrün) (Fig. 3,5) wechselnd.

Sowohl bei Primus II Xanthaurea als bei Primus II Xanthalba und bei Röntgenmutation II (gelbgrün) kommen, wenn auch weniger oft, Chromatophoren mit »weissen Flecken» vor.

Wir fassen das Gesagte folgendermassen zusammen:

1) Die Chromatophoren der Mutanten: Röntgenmutation I (weiss) und Primus II »gulvit» sind stark degeneriert.

2) Die Chromatophoren der Mutanten: Primus II Xanthaurea und Röntgenmutation II (gelbgrün) sind im Vergleich mit Normalchromatophoren verhältnismässig wenig verändert.

3) Die Chromatophoren der Mutante von Primus II Xanthalba sind zwar gut ausgebildet, aber verhältnismässig klein und variieren sowohl bezüglich Form als Grösse.

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ZUR GENETIK VON PHASEOLUS VULGARIS

XII. ÜBER DIE VERERBUNG DER BLÜTEN- UND STAMMFARBE

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(With a summary in English)

HISTORIK.

DIE ersten Untersuchungen über die Vererbung der Blütenfarbe bei der Gartenbohne dürften von E. v. TSCHERMAK (1901) veröffentlicht worden sein. In seiner ersten Arbeit, in der die Merkmale der Mischlinge (F_1) untersucht werden, konstatiert er in zwei Kreuzungen Dominanz der hellila bis dunkelvioletten Farbe über Weiss. Es scheinen alle Übergänge von hellila bis dunkelviolett vorgekommen zu sein, wenigstens hat E. v. TSCHERMAK keine sicheren Grenzen zwischen verschiedenen Nuancen ziehen können.

Die erste Kreuzung wurde ausgeführt zwischen Weisse, gelbhülsige Wachsschwert mit weissen Blüten und Non plus ultra mit lila Blüten. F_1 zeigte dunkler gefärbte Blüten als Non plus ultra. In der zweiten Generation fand E. v. TSCHERMAK (1902) eine Spaltung im Verhältnis 26 dunkellila : 28 lila : 25 blasslila : 19 weiss. Zwischen den dunkellila und blasslila gefärbten gab es alle Übergänge. Es resultiert also eine Spaltung 79 gefärbt : 19 weiss; demnach wahrscheinlich eine monohybride Spaltung. Für eine solche wäre zu erwarten: 73,50 gefärbt : 24,50 weiss. Für das gefundene Verhältnis ist D/m (für 3 : 1) = 1,28.

E. v. TSCHERMAKs zweite Kreuzung wurde ausgeführt zwischen Mettes extrabreite Schlachtschwert mit weissen Blüten und Wachsdattel mit hellila Blüten und ergab analoge Resultate wie in seiner ersten Kreuzung. F_1 hatte dunkellila Blüten; F_2 zeigte Spaltung im Verhältnis 23 dunkellila—lila : 19 blasslila : 13 weiss, also 42 gefärbt : 13 weiss. D/m ist hier für das Spaltungsverhältnis 3 gefärbt : 1 weiss = 0,23.

E. v. TSCHERMAKs Untersuchungen zeigen also nur, dass die lila Blütenfarbe über die weisse dominiert und dass diese in F_2 monohybride Spaltung im Verhältnis 3 gefärbt : 1 weiss geben.

EMERSON (1904) konstatiert die gleichen Erscheinungen wie E. v. TSCHERMAK. Also Unsicherheit in bezug auf Abgrenzung ver-

schiedener Nuancen der farbigen Blüten, Dominanz von gefärbt über weiss und monohybride Spaltung in F_2 im Verbältnisse 3 gefärbt : 1 weiss. Hierfür findet er in drei Kreuzungen zusammen das Verhältnis 75 gefärbt : 30 weiss. D/m für 3 : 1 beträgt hier 0,85. In F_3 haben die weissblütigen Individuen nur wieder solche Nachkommen gegeben, die gefärbtblütigen gaben entweder wieder nur solche oder spalteten in gefärbte und weisse auf, so wie dies theoretisch zu erwarten gewesen ist.

Im übrigen schreibt EMERSON l. c.: »White color of flowers is correlated with white seed color and usually the darker the seed color the deeper the flowers are colored. Where seeds are white with but a small amount of color about the eye, the flowers are also sometimes white. Practically the same results can therefore be secured by a study of seed color as from a study of flower color». Laut EMERSON haben also weissblütige Rassen auch weisse Samen und die Dunkelheit der Blütenfarbe soll mit derjenigen der Testafarbe parallel gehen. Teilfarbige Samen (siehe LAMPRECHT 1934) sollen laut EMERSON mitunter weisse Blüten haben.

JOHANNSEN (1909) teilt die Ergebnisse einer Kreuzung zwischen einer weissblütigen, gelbsamigen Bohnenrasse mit einer violettblütigen, schwarzsamigen mit. In F_2 resultierte folgendes:

Gefunden:	293	schwarzsamig violettblütig	: 105	violettsamig violettblütig	: 121	bronzesamig weissblütig	: 39	gelbsamig weissblütig	
Erwartet:	313,87	»	: 104,62	»	: 104,62	»	: 34,87	»	
D/m für 9 : 3 : 3 : 1 =	1,78		0,04		1,78		0,72		

Hier wird zum erstenmal eine sichere Beziehung zwischen gewissen Farben der Testa und der Blüte nachgewiesen. Wie ich habe zeigen können (LAMPRECHT 1932 a, S. 207—208), entsprechen JOHANNSENS Testafarben folgenden Genotypen (und Farbenbezeichnungen):

PP CC JJ gg BB VV Schwarz
PP CC JJ gg bb VV Veilchenviolett
PP CC JJ gg BB vv Münzbronze
PP CC JJ gg bb vv Schamois (= gelbsamig)

Damit war auch die pleiotrope Wirkung des Gens *V* auf die Blüten- und Testafarben nachgewiesen; eine Erscheinung, die von mir in allen seither untersuchten Kreuzungen hat bestätigt werden können. Alle Bohnenrassen mit *V* haben Bischofsviolette Blüten, aber — je nach der übrigen genotypischen Konstitution — verschiedene Testafarben.

Eine beträchtliche Anzahl von Kreuzungsresultaten in bezug auf die Blütenfarbe ist von J. K. SHAW (1913) veröffentlicht worden. Dieser

Forscher berichtet über das Vorkommen von vier verschiedenen Blütenfarben unter den zu den Kreuzungen benutzten Sorten, nämlich: white, light pink, pink und crimson. In den Kreuzungen ist noch eine weitere, fünfte Farbe, waxy pink, erschienen. Von diesen fünf Blütenfarben entsprechen die ersten drei zweifellos den von mir weiter unten mit Weiss, Laeliafarbig (= light pink) und Bischofsviolett (= pink) bezeichneten. Dies hat nicht nur mit Hilfe von SHAWs Beschreibungen und Abbildungen sondern auch und vor allem durch Anbau und Vergleich mehrerer der von ihm benutzten Sorten festgestellt werden können. SHAWs Sorte Blue Pod Butter mit der Blütenfarbe crimson habe ich mir leider nicht beschaffen können, weshalb ich mich über diese sowie auch über die von ihm in Kreuzungen erhaltene Farbe waxy pink nicht mit Bestimmtheit äussern kann. Jedenfalls können diese Farben — laut SHAWs Beschreibung und Abbildung zu urteilen — nicht mit den von mir als »mit Terminalverstärkung» bezeichneten Blütenfarben identisch sein. Bei den crimson-blütigen Pflanzen sind der Stamm und die Blätter laut SHAW tiefpurpurfarbig, bei den waxy pink-blütigen Pflanzen haben sie ein wachsig-bräunlichgelbes Aussehen, was bei den von mir als »mit Terminalverstärkung» bezeichneten Pflanzen, ausser der abweichenden Blütenfarbe, auch nicht vorkommt.

In bezug auf SHAWs Kreuzungsergebnisse muss leider gesagt werden, dass die Mehrzahl derselben sich infolge der geringen Individuenanzahl oder auf Grund unklarer Spaltungen nicht oder nur schlecht zu einer Faktorenanalyse eignen. Ein Teil derselben berechtigt indessen zweifellos zu einer Analyse und zu Schlusssätzen über die genischen Grundlagen der Blütenfarbe. SHAW hat nun in seiner Arbeit (l. c.) die erhaltenen Spaltungszahlen nur tabellarisch mitgeteilt ohne eine Analyse vorgenommen zu haben. Auch KOOIMAN (1931) hat es in seinem »Monograph of the Genetics of *Phaseolus*» offenbar nicht der Mühe wert gefunden eine solche vorzunehmen. Im folgenden soll daher, soweit das Material dies berechtigt erscheinen lässt, eine Diskussion und Analyse von SHAWs Kreuzungen vorgenommen werden. Bei der Diskussion der Resultate werden die Spaltungszahlen beider Richtungen jeder Kreuzung — die von SHAW gesondert aufgeführt werden — vereinigt behandelt.

SHAW berichtet über 11 Kreuzungen zwischen Weiss und Laeliafarbig. In 9 Kreuzungen war F_1 Laeliafarbig in einer Bischofsviolett (über eine wird bzgl. F_1 nichts erwähnt). Unter den ersterwähnten 9 Kreuzungen sind in F_2 offenbar zwei verschiedene Spaltungstypen

aufgetreten. Die zwei Kreuzungen mit der grössten Individuenanzahl haben ergeben:

Burpee Stringless × *Red Valentine*
Gefunden: 111 Laeliafarbig : 30 Weiss
Erwartet: 105,75 » : 35,25 »
D/m für 3 : 1 = 1,02 (für 9 : 7 würde D/m = 5,38 sein!)

Giant Stringless × *Golden Eyed Wax*
Gefunden: 122 Laeliafarbig : 87 Weiss
Erwartet: 117,56 » : 91,44 »
D/m für 9 : 7 = 0,62 (für 3 : 1 würde D/m = 5,54 sein!)

Im ersten Falle liegt also offenbar monohybride Spaltung nach 3 Laeliafarbig : 1 Weiss vor, im zweiten dagegen dihybride nach 9 Laeliafarbig : 7 Weiss. Das zweite Spaltungsergebnis spricht für das Vorhandensein eines Grundfaktors, dessen Anwesenheit in dominanter Form erforderlich ist, wenn es überhaupt zur Ausbildung von Blütenfarbe kommen können soll, sowie für das Bestehen eines Farbgens für die Ausbildung von Laeliafarbigen Blüten. Nur bei Anwesenheit beider in dominanter Form kann es zur Ausbildung von Blütenfarbe kommen. Mit dieser Annahme ist auch die erste Kreuzung zu erklären, wobei allerdings vorläufig nicht entschieden werden kann, ob es sich bei dieser um eine Spaltung in dem einen oder anderen der beiden Gene handelt.

In einer Kreuzung, *Keeney Rustless* × *Burpee Stringless*, sind in F_2, F_3 und F_4 Individuen mit Bischofsvioletten Blüten aufgetreten, während F_1 als Laeliafarbig klassifiziert worden ist. Dies widerspricht allen bisherigen und auch meinen umfangreichen Untersuchungsresultaten und dürfte entweder auf eine spontane Einkreuzung oder fehlerhafte Klassifikation von F_1 zurückzuführen sein. Die Gesamtindividuenanzahl in F_2 hat nur 37 betragen.

In einer Kreuzung Laeliafarbig × Weiss hat F_1, wie früher erwähnt worden ist, Bischofsviolette Blüten getragen. In F_2 dieser Kreuzung, *Warwick* × *Creaseback*, wurde folgende Spaltung erhalten:

Gefunden: 81	Bischofsviolett : 16	Laeliafarbig : 13	Weiss
Erwartet: 61,87	» : 20,62	» : 27,50	»
D/m für			
9 : 3 : 4 = 3,68	1,13	3,19	

Die gefundenen Zahlen zeigen sehr schlechte Übereinstimmung an. Trotzdem ist, wie aus meinen Untersuchungen hervorgehoben wird, kaum eine andere Spaltung anzunehmen. Diese Spaltung spricht für

das Bestehen eines weiteren Genpaares, nämlich für die Ausbildung der Blütenfarbe Bischofsviolett kontra Laeliafarbig bzw. Weiss. In der in Frage stehenden Kreuzung ist offenbar der weissblütige Elter Träger dieses Gens in dominanter Form gewesen, hat aber überdies den Grundfaktor für die Ausbildung von Farbe in rezessiver Form enthalten.

Nach Kreuzung von Bischofsviolett × Weiss hat F_1 stets Bischofsviolette Blüten gezeigt. SHAW führt 11 solche Kreuzungen an. Die meisten der erhaltenen Spaltungsresultate können indessen nicht diskutiert werden. Zwei Spaltungstypen scheinen aber unterschieden werden zu können, nämlich eine Spaltung in nur Bischofsviolett und Weiss und eine in Bischofsviolett, Laeliafarbig und Weiss. Einige der mitgeteilten Spaltungszahlen könnten als dihybrid 9 : 7 bzw. 9 : 3 : 4 aufgefasst werden. Von einer Wiedergabe derselben nehme ich Abstand, da die Zahlen teils zu klein sind, teils zu grosse Abweichungen von den erwarteten Verhältnissen aufweisen.

Kreuzungen zwischen Sorten mit den Blütenfarben Bischofsviolett und Laeliafarbig wurden von SHAW fünf angeführt. F_1 hat Bischofsviolette Blüten entwickelt. F_2 hat stets nur in Individuen mit Bischofsvioletten und Laeliafarbigen Blüten gespaltet. Wahrscheinlich hat es sich in allen Fällen um monohybride Spaltung, dem Verhältnis 3 Bischofsviolett : 1 Laeliafarbig entsprechend, gehandelt. Ein Beispiel sei angeführt.

Burpee Stringless × *German Black Wax*
Gefunden: 127 Bischofsviolett : 42 Laeliafarbig
Erwartet: 126,75 » : 42,25 »
D/m für 3 : 1 = 0,04

Hier besteht also geradezu ausgezeichnete Übereinstimmung zwischen den gefundenen und den theoretisch erwarteten Spaltungszahlen.

In dieser Kreuzung haben also beide Eltern den Grundfaktor für die Ausbildung von Blütenfarbe in dominanter Form besessen. Die Spaltungsergebnisse sprechen ferner dafür, dass für den Unterschied Bischofsviolett—Laeliafarbig ein Genpaar verantwortlich ist.

Weiter teilt SHAW die Resultate von 9 Kreuzungen zwischen verschiedenen Weissblütigen Rassen mit. F_1 dieser Kreuzungen hat entweder Weisse, Laeliafarbige oder Bischofsviolette Blüten gehabt. Mit Hinblick auf den bereits früher besprochenen Grundfaktor für die Ausbildung von Blütenfarbe sind diese Ergebnisse auch zu erwarten gewesen. Von einer Wiedergabe von Spaltungszahlen nehme ich auch hier Abstand, da sie zu einer Faktorenanalyse nicht oder kaum zu ver-

wenden sein dürften. Wie zu erwarten gewesen ist, haben die Weissblütigen F_1-Pflanzen ausschliesslich Weissblütige Nachkommen gegeben, die Laeliafarbigen und Bischofsvioletten haben wieder Aufspaltung in Weissblütige und Farbige gezeigt.

Schliesslich sind die Resultate von SHAWs Kreuzungen mit der Sorte Blue Pod Butter mit crimson Blütenfarbe zu besprechen. SHAW charakterisiert diese Blütenfarbe folgendermassen: »The so-called crimson flowers of the Blue Pod Butter are more properly a purplish crimson, and invariably the leaves and stems of the plants are deeply tinged with dark purple. These flowers are distinguished from the pink ones, not only by their darker shade but more certainly by the outside of the banner petal which is purplish crimson instead of uncolored». Die letzte Äusserung dürfte — auch mit Hinblick auf SHAWs colorierte Tafel — insofern einer Berichtigung bedürfen, als die Aussenseite der Fahne der Bischofsvioletten Blüten keineswegs »uncolored» sondern nur viel schwächer gefärbt ist als die Innenseite oder die Fahnenaussenseite von SHAWs crimson-Blüten. In gleicher Weise wie sich crimson von Bischofsviolett (pink) unterscheidet, unterscheidet sich waxy pink von Laeliafarbig (light pink), d. h. dieselbe Verstärkung der Farbe die crimson gegenüber Bischofsviolett darstellt, zeigt waxy pink gegenüber Laeliafarbig.

SHAW (l. c.) veröffentlicht 6 verschiedene Kreuzungen zwischen crimson und Weiss. Unter diesen scheinen wenigstens zwei verschiedene Typen von Aufspaltung vorzukommen. F_1 zeigte gewöhnlich die Farbe crimson (in zwei Kreuzungen jedoch die Farbe Bischofsviolett!). Die beiden folgenden Beispiele illustrieren die F_2-Spaltungstypen.

Blue Pod Butter × *Davis Wax*

Gefunden:	52	crimson :	20	Bischofsviolett :	24	Weiss	
Erwartet:	54,0	» :	18,0	» :	24,0	»	
D/m für 9 : 3 : 4 =	0,41		0,52		0,0		

Es besteht gute Übereinstimmung zwischen den gefundenen Spaltungszahlen und den für eine dihybride Spaltung nach dem Verhältnis 9 : 3 : 4 erwarteten.

Blue Pod Butter × *Golden Eyed Wax*

Gefunden:	44	crimson :	12	Bischofsviolett :	13	waxy pink :	3	Laeliafarbig :	41	Weiss
Erwartet:	48,53	» :	16,17	» :	16,17	» :	5,39	» :	28,72	»
D/m für 27 : 9 : 9 : 3 : 16 =	0,85		1,12		0,85		1,05		2,62	

In diesem Falle finden wir befriedigende Übereinstimmung zwischen dem gefundenen und dem theoretisch angenommenen Spaltungsverhältnis.

Diese Befunde von SHAW berechtigen zur Annahme eines Gens, das in dominanter Form die Blütenfarbe Bischofsviolett in crimson und Laeliafarbig in waxy pink umwandelt. Auf die weissblütigen Formen scheint dieses Gen dagegen keinen Einfluss zu haben. Parallel mit der Veränderung der beiden Blütenfarben Bischofsviolett und Laeliafarbig durch das erwähnte Gen geht auch eine Veränderung der Färbung von Blättern und Stamm einher; Pflanzen mit crimson Blütenfarbe zeigen laut SHAW tiefpurpurfarbige Blätter und Stamm, die mit waxy pink Blütenfarbe zeigen ein wachsig-bräunlichgelbes Aussehen. Hier scheint demnach eine ausgesprochen pleiotrope Wirkung des in Frage stehenden Gens vorzuliegen.

SHAW (l. c.) veröffentlicht noch 5 Kreuzungen zwischen crimson und Laeliafarbig und 4 Kreuzungen zwischen crimson und Bischofsviolett. Die erhaltenen Spaltungsresultate stehen mit der eben diskutierten Annahme in Übereinstimmung. So zeigte F_1 in allen diesen Fällen crimson Blüten. In F_2 der Kreuzungen crimson $\times$ Laeliafarbig erfolgte eine Spaltung in die vier Farben crimson, Bischofsviolett, waxy pink und Laeliafarbig, also ganz wie zu erwarten gewesen ist. SHAWs Zahlen der in Frage stehenden fünf Kreuzungen können jedoch kaum zu einer zahlenmässigen Analyse verwendet werden. F_2 der Kreuzungen crimson $\times$ Bischofsviolett schliesslich spaltete in allen vier Fällen nach dem monohybriden Verhältnis 3 crimson : 1 Bischofsviolett. Ein Beispiel sei angeführt.

Blue Pod Butter $\times$ *Challenge Black Wax*
Gefunden: 226 crimson : 87 Bischofsviolett
Erwartet: 234,75 » : 78,25 »
D/m für 3 : 1 = 1,14

Es besteht demnach vollkommen befriedigende Übereinstimmung mit der theoretischen Erwartung. Auch die übrigen drei Kreuzungen zwischen crimson und Bischofsviolett haben entsprechende Zahlen geliefert. Hierbei glaube ich davon absehen zu können, dass in oben angeführter Kreuzung überdies zwei Individuen als Laeliafarbig und in einer anderen Kreuzung 10 Individuen als Weiss klassifiziert worden sind. Wahrscheinlich hat es sich bei diesen wenigen Ausnahmen um spontane Kreuzungen gehandelt.

TJEBBES und KOOIMAN (1921) berichten über die Aufspaltung eines

spontanen Bastards. Die Mutterpflanze des Bastards gehörte der holländischen Sorte Stockievitsboon (= de Pragues marbré à rames) an. Als Vatersorte konnten die Verfasser Haricot blanc nain de la Haye bestimmen. Erstere Sorte hat Laeliafarbige Blüten, letztere Weisse. Der Bastard (F_1) zeigte Bischofsviolette Blüten (violette) und in F_2 wurde folgende Aufspaltung in der Blütenfarbe festgestellt:

10 violet foncé : 12 violet clair : 10 lilas : 11 blanc.

KOOIMAN (1931) fasst diese Spaltung als 23 Violett (dunkel oder hell) : 10 Lila : 11 Weiss, dem Verhältnis 2 : 1 : 1 entsprechend, auf. Wie meine unten zu besprechenden Untersuchungen zeigen werden, hat es sich hier wahrscheinlich um eine dihybride Spaltung im Verhältnis 9 : 3 : 4 gehandelt, dem folgenden Schema entsprechend.

Gefunden:	23 Bischofsviolett	: 10 Laeliafarbig	: 11 Weiss
Erwartet:	24,75 »	: 8,25 »	: 11,0 »
D/m für			
9 : 3 : 4 =	0,53	0,67	0,0

Wie ersichtlich zeigen bei dieser Annahme die gefundenen Zahlen gute Übereinstimmung mit den für das Verhältnis 9 : 3 : 4 zu erwartenden. Die Zahlen sind allerdings zu klein, um als sicher betrachtet werden zu können.

TJEBBES und KOOIMAN (l. c.) konstatieren ferner einen bestimmten Zusammenhang zwischen der Bischofsvioletten Blütenfarbe und den dunkleren Testafarben. Ferner wird von ihnen hier wohl das erstemal hervorgehoben, dass die dunkler violette Blütenfarbe den Homozygoten, die heller violette den Heterozygoten entspricht, indem sie sagen (l. c. p. 48): »Dans les fleurs une différence existe, les homozygotes possèdent une couleur violette indubitablement plus foncée que les hétérozygotes». Es handelt sich hier wohl sicher um die beiden Formeln *VV* und *Vv*.

In einer weiteren Arbeit schreiben TJEBBES und KOOIMAN (1922), dass der Faktor, der schwarze und schwärzliche Testafarbe (bei gleichzeitiger Anwesenheit gewisser anderer Faktoren) verursacht, auch blasslila (lilas pâle) Blütenfarbe bedingt. Vermutlich sollte es hier wohl Violette Blütenfarbe heissen! Denn unter den sechs bisher bekannten Farbgenen für die Testa (abgesehen von Grundgen und Modifikationsgenen, die selbst keine Testafarbe bedingen) verursacht nur das Gen *V* gleichzeitig Blütenfarbe, und zwar Bischofsviolett. Linien mit irgend welchen Kombinationen der übrigen fünf Farbgene können sowohl Weisse wie auch Laeliafarbige Blüten, aber — soweit bisher bekannt — niemals Bischofsviolette Blüten haben. Ferner schreiben TJEBBES und

KOOIMAN (l. c.): »Sous l'influence d'un facteur, que nous avons nommé *G*, la couleur lilas des fleurs se change en violet foncé». Auch hier dürfte es sich mit aller Bestimmtheit um das Gen *V* handeln. Die gleiche Erscheinung ist schon, wie früher erwähnt worden ist, von JOHANNSEN (1909) festgestellt worden. TJEBBES und KOOIMAN sagen ferner, dass für die Ausbildung der Laeliafarbigen Blüte (couleur lilas de la fleur) ein Faktor verantwortlich sein muss, der wahrscheinlich keinen Einfluss auf die Färbung der Testa hat.

Schliesslich zitieren TJEBBES und KOOIMAN eine Angabe von SHAW and NORTON (1918), laut der teilfarbige (»geäugte») Bohnenrassen stets weisse Testa haben sollen. Ausgenommen sollten Fälle sein, in denen das Auge sehr gross ist.

Im Jahre 1930 veröffentlichten MIYAKE, IMAI und TABUCHI als erste Untersuchungen über die Vererbung der Stammfarbe. Gleichzeitig wurde u. a. auch die Vererbung der Blütenfarbe studiert. Diese Verfasser bezeichnen die Blütenfarbe Bischofsviolett mit Red und Laeliafarbig mit Pink. In bezug auf die Vererbung der Blütenfarbe können sie teils schon von anderen Forschern gefundene Spaltungsresultate bestätigen, teils berichten sie über einen neuen Typus mit »fleckigen» Blüten und seine Vererbung. Für die drei Blütenfarben Bischofsviolett, Laeliafarbig und Weiss teilen sie folgende Spaltungsverhältnisse mit.

Gefunden: 253 Bischofsviolett : 76 Laeliafarbig
Erwartet: 246,75 » : 82,25 »
D/m für 3 : 1 = 0,80

Gefunden: 46 Bischofsviolett : 11 Weiss
Erwartet: 42,75 » : 14,25 »
D/m für 3 : 1 = 0,99

In beiden Fällen stimmen die gefundenen Zahlen gut mit dem monohybriden Verhältnis 3 : 1 überein. Den ersten Fall finden wir bei SHAW (1913), den letzteren bei JOHANNSEN (1909).

Der »fleckige» Typus ist besser als »gestrichelt» zu bezeichnen, denn die Fleckigkeit besteht aus kurzen farbigen (Bischofsviolett bzw. Laeliafarbig) Strichelchen längs den Nerven der Flügel der Blüte. Im übrigen sind Flügel und Fahne Weiss. Ich besitze selbst mehrere Linien mit diesem Blütentypus. Nach Kreuzung dieses Typus mit Bischofsviolett-blütigen (1. Fall) bzw. Laeliafarbigen (2. Fall) fanden MIYAKE, IMAI und TABUCHI in F_2 zwei verschiedene Spaltungsverhältnisse, nämlich:

Gefunden: 434 Bischofsviolett : 125 Gestrichelt
Erwartet: 419,25 » : 139,75 »
D/m für 3 : 1 = 1,44

Gefunden: 220 Bischofsviolett : 63 Laeliafarbig : 88 Gestrichelt
Erwartet: 208,68 » : 69,56 » : 92,75 »
D/m für
9 : 3 : 4 = 1,19 0,87 0,57

Auch diese beiden Spaltungsverhältnisse zeigen gute Übereinstimmung zwischen den gefundenen und den theoretisch berechneten Werten. Sie scheinen zu dem Schlusssatz zu berechtigen, dass die Strichelung sich nur auf im übrigen Weissen Blüten geltend macht. Denn unter den Bischofsvioletten und Laeliafarbigen Blüten kamen, soweit aus der zitierten Arbeit hervorgeht, keine überdies gestrichelten Blüten vor. Die Ausbildung der Strichelung, wenigstens einer okulär wahrnehmbaren, scheint also durch die Anwesenheit der beiden erwähnten Blütenfarben verhindert zu werden oder sie wird durch diese nur verdeckt. Gegenüber Weisser Blütenfarbe erscheint die Strichelung dominant, gegenüber ganzgefärbten Blüten rezessiv. MIYAKE, IMAI und TABUCHI sagen: »The flecked flower behaves as a simple recessive to the coloured flower».

Stammfarben werden von diesen Forschern drei verschiedene beschrieben, nämlich Rot (red stem, coloured intensely), Rosa (pink stem, coloured dilutely) und Grün (green stem, without anthocyanin pigment). Folgende Kreuzungstypen wurden ausgeführt: 1) Rot × Rosa, 2) Rosa × Grün, 3) Rot × Grün, und 4) Grün × Grün. In allen Fällen hat Rot über Rosa und Grün bzw. Rosa über Grün dominiert. Nach Kreuzung von Rosa × Grün und Grün × Grün wurde eine Rote F_1-Generation erhalten. In den vier Kreuzungstypen wurden folgende Spaltungstypen erhalten.

1) *Rot* × *Rosa* (6 Kreuzungen)
Gefunden: 604 Rot : 199 Rosa
Erwartet: 602,25 » : 200,75 »
D/m für 3 : 1 = 0,14

2) *Rosa* × *Grün* (4 Kreuzungen)
Gefunden: 304 Rot : 79 Rosa : 116 Grün
Erwartet: 280,68 » : 93,56 » : 124,75 »
D/m für
9 : 3 : 4 = 2,10 1,67 0,91

3) *Rot* × *Grün* (4 Kreuzungen)

Gefunden: 496 Rot : 145 Grün
Erwartet: 480,75 » : 160,25 »
D/m für 3 : 1 = 1,39
Gefunden: 232 Rot : 73 Rosa : 93 Grün
Erwartet: 223,87 » : 74,62 » : 99,50 »
D/m für
9 : 3 : 4 = 0,82 0,21 0,75

4) *Grün* × *Grün* (2 Kreuzungen)

Gefunden: 409 Rot : 270 Grün
Erwartet: 381,94 » : 297,06 »
D/m für 9 : 7 = 2,09

In sämtlichen mitgeteilten Fällen besteht zwischen den gefundenen und den theoretisch berechneten Spaltungszahlen gute bzw. befriedigende Übereinstimmung. Die mitgeteilten Spaltungszahlen zeigen, dass für die Ausbildung der drei Stammfarben wenigstens drei Genpaare verantwortlich sind, worauf jedoch später zurückgekommen werden soll.

Bei der gemeinsamen Untersuchung von Stamm- und Blütenfarbe haben MIYAKE, IMAI und TABUCHI feststellen können, dass die Rote Stammfarbe immer mit Bischofsvioletten Blüten und die Rosa Stammfarbe stets mit Laeliafarbigen Blüten einhergeht. Grüne Stammfarbe kann jedoch mit einer beliebigen der erwähnten Blütenfarben Bischofsviolett, Laeliafarbig, Gestrichelt und Weiss kombiniert auftreten. Für die Spaltung der Blütenfarben innerhalb der Individuengruppe mit grünem Stamm teilen sie nur ein monohybrides Verhältnis, nämlich 3 Bischofsviolett : 1 Laeliafarbig mit.

Von Interesse für das Studium der Vererbung der Blütenfarbe ist ferner, dass diese Forscher ein Defizit für weissblütige Individuen finden. Sie sagen diesbezüglich: »The deficit in the white flowers seems due to their low viability». Ein Zusammenhang zwischen Blüten- und Stammfarbe einerseits und Testafarbe andererseits ist aus der Arbeit von MIYAKE, IMAI und TABUCHI nicht zu entnehmen.

Vor kurzem erschien eine Arbeit von PRAKKEN (1934), in der eine Kreuzung, Fijne tros × Wagenaar, einem eingehenden Studium unterzogen worden ist. PRAKKEN beweist beim Studium der Vererbung der Testafarbe folgende genotypische Konstitution: Fijne tros = *pp VV*, Wagenaar = *PP vv*. Dementsprechend erhält er in F_2 folgende Spaltung in bezug auf die Blütenfarbe.

Gefunden:	1876	Bischofsviolett	: 540	Laeliafarbig	: 816	Weiss
Erwartet:	1818	»	: 606	»	: 808	»
D/m für 9 : 3 : 4 =	2,06		2,97		0,32	

Trotz der wenig guten Übereinstimmung zwischen den gefundenen und den berechneten Spaltungszahlen dürfte es sich zweifellos um das angenommene dihybride Spaltungsverhältnis 9 : 3 : 4 handeln. Die von PRAKKEN bei Rückkreuzungen erhaltenen Resultate sprechen auch hierfür. Die obigen Spaltungszahlen bestätigen also JOHANNSENS (1909) Resultat, dass der für gewisse Testafarben verantwortliche Faktor *V* auch Bischofsviolette Blütenfarbe bedingt. In PRAKKENS Kreuzung hatten ferner alle weisssamigen Individuen (*pp*) auch weisse Blütenfarbe. Gleichwie TJEBBES und KOOIMAN (1921) findet PRAKKEN, dass die in *V* heterozygoten Individuen eine etwas hellere Bischofsviolette Blütenfarbe aufweisen.

Fassen wir kurz zusammen was bisher über die Vererbung der Blütenfarben bei *Phaseolus vulgaris* bekannt geworden ist.

1. Gefärbte Blüten dominieren stets über weisse. Dies gilt für alle bisher untersuchten Blütenfarben und ist in sämtlichen veröffentlichten Arbeiten bestätigt worden.

2. Zwei Forscher (E. v. TSCHERMAK 1901, 1902 und EMERSON 1904) finden, dass die gefärbten Blüten in ihrer Farbe von blasslila bis dunkelviolett variieren und dass zwischen den Nuancen keine scharfe Grenze gezogen werden kann. EMERSON (1904) sagt: »Usually the darker the seed color the deeper the flowers are colored».

3. Dunklere Blütenfarben dominieren stets über hellere. Diese Dominanz scheint aber keine vollkommene zu sein, indem die Heterozygoten nicht ganz so dunkle Farbe aufweisen wie die Homozygoten (TJEBBES und KOOIMAN 1921, PRAKKEN 1934).

4. Bisher sind folgende Blütenfarben festgestellt bzw. auf ihre Vererbung untersucht worden:

Bischofsviolett [Dunkelviolett? (E. v. TSCHERMAK 1901, 1902), Violett (JOHANNSEN 1909), pink (SHAW 1913, SHAW and NORTON 1918), violet foncé, violet clair (TJEBBES und KOOIMAN 1921, 1922), red (MIYAKE, IMAI and TABUCHI 1930), Bischofsviolett (LAMPRECHT 1932 a), violet, Bishopsviolet (PRAKKEN 1934)].

Laeliafarbig [Blasslila, Lila? (E. v. TSCHERMAK 1901, 1902), light pink (SHAW 1913, SHAW and NORTON 1918), lilas (TJEBBES und

KOOIMAN 1921, 1922), pink (MIYAKE, IMAI and TABUCHI 1930), Laeliafarbig (LAMPRECHT 1932 b)].

Weiss (Sämtliche Verfasser).

Crimson (SHAW 1913).

Waxy pink (SHAW 1913).

Gestrichelt — Bischofsviolett oder Laeliafarbig: »flecked» (MIYAKE, IMAI and TABUCHI 1930).

5. Die Farbe Bischofsviolett geht stets mit gefärbter Testa parallel, und zwar scheinen nur gewisse Testafarben in Betracht zu kommen (JOHANNSEN 1909, TJEBBES und KOOIMAN 1921, 1922). Verantwortlich hierfür ist das Genpaar *V*—*v*, *V*-Pflanzen haben Bischofsviolette, *v*-Pflanzen Weisse Blütenfarbe (LAMPRECHT 1932 a, PRAKKEN 1934). *VV*-Pflanzen sind dunkler Bischofsviolett als *Vv*-Pflanzen (TJEBBES und KOOIMAN 1921, PRAKKEN 1934).

6. Für Laeliafarbig ist ein besonderes Gen verantwortlich, in bezug auf das TJEBBES und KOOIMAN (1922) sagen, dass es wahrscheinlich keinen Einfluss auf die Färbung der Testa hat. Laeliafarbig wird durch *V* — laut den gleichen Verfassern, die die Bezeichnung *G* verwenden — in Bischofsviolett umgewandelt.

7. Bohnenrassen mit teilfarbiger Testa (siehe LAMPRECHT 1934) sollen Weisse Blütenfarbe haben (EMERSON 1904, SHAW and NORTON 1918).

8. Das Grundgen *P* für die Ausbildung von Testafarbe (siehe LAMPRECHT 1932 a) scheint auch Bedingung für die Ausbildung von Blütenfarbe zu sein (PRAKKEN 1934).

9. Das Verhalten der beiden Genpaare für Blütenfarbe (Bischofsviolett—Weiss, *V*—*v*, und Laeliafarbig—Weiss) zueinander sowie zum Grundgen *P* und zu den beiden Genen für die Ausbildung von teilfarbiger Testa *t* und *e* erscheint keineswegs klargelegt. *V* soll sowohl allein wie zusammen mit dem Gen für Laeliafarbig Bischofsviolett versachen. Es überrascht da, dass bei Spaltungen in den drei Blütenfarben Bischofsviolett, Laeliafarbig und Weiss niemals das zu erwartende Spaltungsverhältnis 12 Bischofsviolett : 3 Laeliafarbig : 1 Weiss gefunden worden ist, sondern stets das Verhältnis 9 Bischofsviolett : 3 Laeliafarbig : 4 Weiss (SHAW 1913, TJEBBES und KOOIMAN 1921, MIYAKE, IMAI and TABUCHI 1930, PRAKKEN 1934). Es könnte sich hier also auch um unilokale Faktoren handeln, und das letztgenannte Spaltungsverhältnis (9 : 3 : 4) würde dann eine Spaltung im Grundgenpaar *P*—*p* und einem Paar der unilokalen Faktoren darstellen.

10. Für die beiden Blütenfarben crimson und waxy pink (SHAW

1913) besteht ein Gen, das zusammen mit Bischofsviolett die erstere, mit Laeliafarbig die letztere dieser Farben bedingt.

11. Der gestrichelte Blütentypus dominiert über Weiss. Bei gefärbten Blüten tritt er nicht in Erscheinung (MIYAKE, IMAI and TABUCHI 1930).

In bezug auf die Stammfarben ist bisher folgendes bekannt (MIYAKE, IMAI and TABUCHI 1930):

1. Es bestehen drei verschiedene Stammfarben: Rot, Rosa und Grün. Rot dominiert über Rosa und Grün, Rosa über Grün.

2. Gleichwie für die Blütenfarbe besteht ein Grundgen für die Ausbildung der Stammfarbe, das wahrscheinlich mit *P* identisch ist.

3. Rote Stammfarbe soll stets mit Bischofsvioletten Blüten und Rosa Stammfarbe mit Laeliafarbigen Blüten einhergehen. Grüne Stammfarbe soll mit einer beliebigen der bekannten Blütenfarben kombiniert vorkommen können.

HIER BEHANDELTE BLÜTEN- UND STAMMFARBEN.

Die sichere Beurteilung der Blütenfarbe erfordert eine gewisse Übung und Erfahrung. Die diesbezüglichen Schwierigkeiten gehen u. a. aus den Äusserungen von E. v. TSCHERMAK (1901, 1902) und EMERSON (1904) hervor (siehe Historik). Bei meinen Untersuchungen hat sich herausgestellt, dass die Blütenfarben ebensogut und häufig sicherer im voll entwickelten Knospenstadium bestimmt werden können. Bei Beurteilung der Farbe der Blüten müssen diese neu ausgeschlagen sein. Bei älteren Blüten sind Irrtümer kaum zu vermeiden. Die Blütenfarben verblassen oft recht schnell, ganz besonders bei sehr trockenem Wetter. Auch sollen die Versuche auf offenem Felde und nicht in mehr oder weniger schattigen Lagen ausgeführt werden, da die Blütenfarben durch verschiedenen Lichtgenuss etwas in der Nuance beeinflusst werden.

Im folgenden werden die hier auf ihre Vererbung untersuchten Blüten- und Stammfarben kurz charakterisiert. Zur Festlegung der verschiedenen Farben wurden folgende Farbenarbeiten benutzt: 1. Répertoire de Couleurs publié par la Société française des Chrysanthémistes et RENÉ OBERTHUR, 1905 (= RC), 2. KLINCKSIECK et VALETTE, Code des Couleurs, Paris 1908 (= CC), 3. Color Standards and Nomenclature by ROBERT RIDGWAY, Washington 1912 (= CS) und 4. Farbentafeln nach OSTWALD, bearbeitet von der Deutschen Werkstelle für Farbkunde; Ernst Benary, Erfurt (= FT). Es folgen zuerst die Blütenfarben.

Bischofsviolett. Fahne: Ein helles und lebhaftes Bischofsviolett (bei Homozygotie in *V*). RC 189/1—2, aber lebhafter. CS Light Rosolane Purple, XXVI, 69′ b bis Liseran Purple, XXVI, 67′ b und etwas heller. CC 561 bis 541. FT 11 na bis 10 na. Gegen die Basis zu geht die Farbe der Fahne in Crèmegelb über. Flügel: Wie die Fahne aber etwas heller im Farbenton, etwa CS, XXVI, 67′ b. CC 541. Das Schiffchen ist nur zum Teil schwach violett gefärbt, im übrigen ist es Crèmegelb. Bei in *V* heterozygoten Individuen ist die Farbe von Fahne und Flügel heller, Malvenfarbig, Mauve poupré, RC 186/1 bis Heliotropviolett RC 188/1; FT 11,5 ia bis 11,5 ga; CS Purplish Lilac, XXXVII, 65″ d bis 66″ d, aber mit keiner scharfen Grenze zum gewöhnlichen Bischofsviolett; Übergänge bilden CS XXVI, 67′ c—b bis 66′ c—b. Die Knospen von Bischofsvioletten Blüten schimmern deutlich Schmultziglila durch.

Für die Bischofsvioletten Blüten ist ferner charakteristisch, dass der Kelch an den Stellen, wo er nicht von den Vorblättern bedeckt wird, feine anthocyanfarbige Pünktchen und Fleckchen aufweist (CC 583). Ferner ist der Blütenstiel von mehr oder weniger zahlreichen feinen längsgehenden, kurzen, anthocyanfarbigen Strichelchen bedeckt, die besonders auf der der Sonne zugekehrten Seite deutlich ausgebildet sein können.

Laeliafarbig. Fahne: Blass Laeliafarbig RC 187/1, aber gewöhnlich etwas heller. CS Light Pinkish Lilac bis Pale Laelia Pink, XXXVII, 65″ f—g bis XXXVIII, 67″ f—g. CC 553 B—A. Flügel: Gleiche Farbentöne aber stets mehr oder weniger heller-blasser. CC 528 A. Basis von Fahne und Flügel Crèmegelb. Das Schiffchen ist hell Crèmegelb. Die Knospen von Laeliafarbigen Blüten schimmern sehr blass Schmutziglila durch, sind aber immer deutlich von den rein Crèmefarbigen Knospen der Weissen Blüten zu unterscheiden. Auf dem Kelch, den Vorblättern und den Blütenstielen fehlen hier die bei Bischofsvioletten Blüten vorhandenen anthocyanfarbigen Pünktchen bzw. Strichelchen; wenigstens sind solche bei okularer Besichtigung nicht sicher zu erkennen.

Weiss. Fahne im oberen Teil Reinweiss, nach unten zu in Crèmegelb übergehend. Gleiches gilt hier für die Flügel und für das Schiffchen. Letzteres ist in der obersten Windung etwas grünlichgelb, was übrigens auch für die beiden vorigen Blütenfarben gilt. Knospen rein Crèmefarben. Kelch, Vorblätter und Blütenstiele rein Grünlichgelb (CC 228 D).

Bischofsviolett mit Terminalverstärkung auf der Fahne. Die von mir als Terminalverstärkung bezeichnete Erscheinung kommt sowohl bei Bischofsvioletten, Laeliafarbigen wie auch Weissen Blüten vor. Die

Farbenverstärkung betrifft nur den oberen — nicht auch seitlichen — Rand der Fahne. Die Farbe ist hier, vorzüglich auf der Innenseite, in einer vom Rand abwärts reichenden Breite von 1—2 mm sehr deutlich verstärkt. Nach unten geht die Verstärkung in die gewöhnliche Farbe über. Im Knospenstadium hat dies zur Folge, dass die Spitze der Knospe gefärbt (bei Weissen Blüten) oder bedeutend stärker gefärbt erscheint. Bei Bischofsvioletten Blüten ist die Farbe der Verstärkung Schoenfelds Purple, CS XXVI, 69′ i. CC 557. Die Spitze von Knospen erscheint jedoch erheblich dunkler, etwa Dull Dusky Purple, CS XXVI, 67′ m. In *V* heterozygote Individuen haben auch hier etwas hellere Farbe. Diese Blütenfarbe findet sich bei der französischen Sorte Souvenir de Deuil. Blütenstiele und Kelch wie bei Bischofsviolett, aber intensiver anthocyan-punktiert bzw. -gestrichelt.

Laeliafarbig mit Terminalverstärkung auf der Fahne. Bei dieser Farbe geht der Ton der Verstärkung am Fahnenrand deutlich ins Rötliche. Er entspricht etwa Hell Spinel Pink bis Thulite Pink, CS XXVI, 71′ c—d. RC 181/1, Malvenfarbig, CC 592 mit Übergang zu CC 571. Die Knospen mit deutlich Pink-farbiger Spitze. Auf den Blütenstielen gewahrt man ab und zu Spuren von anthocyanfarbigen Strichelchen (nur unter der Lupe sichtbar). Diese Farbe findet sich bei den Sorten Hinrichs Riesen, Coco marbré u. a.

Weiss mit Terminalverstärkung auf der Fahne. Es ist überraschend, dass diese Färbung des Fahnenrandes auch bei Weissen Blüten auftritt. Sie bildet hier allerdings keine Verstärkung der übrigen Crèmefärbung der Blüte, sondern eine Verstärkung in einer ganz anderen Farbe. Der Fahnenrand ist hier Incarnatrot dunkel, RC 139/1—2, nach unten in reines Weisslich Crème übergehend. CS Flesh Pink, XIII, 5′ e—f. CC 78 D—103 D. Knospen sind bei dieser Blütenfarbe Crèmefarbig mit Incarnatroter Spitze.

Stammfarben kommen nur drei in Frage, nämlich Rot, Rosa und Grün. Abgesehen von der Grünen, nur durch Chlorophyll verursachten Farbe, sind die Stammfarben nicht einheitlich, sondern es wechseln stets Gruppen von Epidermiszellen, die nur Chlorophyll enthalten mit solchen ab, die durch Anthocyan gefärbt sind. Die Verteilung solcher Zellengruppen ist in Fig. 1 ersichtlich. Okulär betrachtet machen die farbigen Zellengruppen den Eindruck von feinen Strichelchen. Die sechseckigen Zellen mit einem Ring in der Mitte (in Fig. 1) sind borstentragende Zellen.

Rot. Die Farbe macht keinen einheitlichen klar Roten Eindruck, sondern man gewahrt, dass es sich um eine Mischfarbe von Grün und

Rot handelt. Der Gesamteindruck ist Haematite Red, CS XXVII 5″ m. Die Farbe kann überdies einen mehr oder weniger graulichen Anstrich aufweisen, was wahrscheinlich auf die Beschaffenheit der Epidermisoberfläche zurückzuführen ist. Nach oben, in der Nähe der Ansatzstelle der Kotyledonen, geht die Farbe in Grün über. Unter der Erde fehlt das Grün fast vollständig, während die Roten Strichelchen in klarer Farbe zutage treten; etwa Dahlia Carmine CS XXVI, 71′ k entsprechend.

Rosa. Verteilung am Stamm und in Zellengruppen wie bei Rot. An den klarsten Stellen ist die Farbe Light Russet-Vinaceous, CS

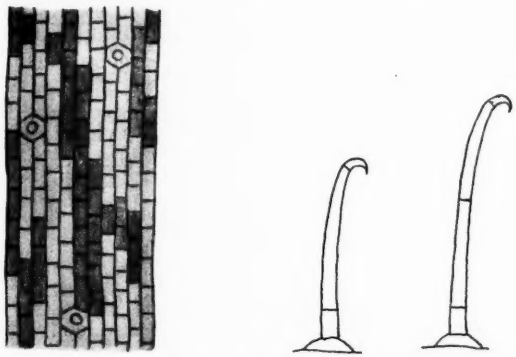

Fig. 1. Links Teil der Epidermis des Stammes einer *Phaseolus*-Pflanze mit Roter Stammfarbe. Die dunkleren Zellen sind durch Anthocyan dunkelpurpur gefärbt. Die sechseckigen Zellen mit einem Kreis in der Mitte sind trichomtragend. Rechts zwei für *Phaseolus* charakteristische Trichome.

XXXIX, 9‴. Diese Farbe zeigt häufig Übergänge zu Schmutzig Chlorophyllgrün. Zweifelhafte Individuen müssen mit der Lupe untersucht werden. Findet man dann Strichelchen in blasser Anthocyanfarbe, so besteht kein Zweifel, dass man es mit Rosa und nicht mit Grün zu tun hat. Hier spielt der früher erwähnte grauliche Anstrich der Epidermisoberfläche eine Rolle.

Grün. Reines Chlorophyllgrün, Biscay Green, CS VXII, 27′ i—h bis Light Cress Green, CS XXXI, 29″ i—h, entsprechend.

KREUZUNGSERGEBNISSE.

Die erste von mir in bezug auf Blütenfarbe analysierte Kreuzung, Nr. 2, wurde ausgeführt zwischen Linie 1 aus der Braunen Bohnensorte Stella mit Laeliafarbigen und Linie 2 aus der Wachsbohnensorte Neger

mit Bischofsvioletten Blüten. Die F_1-Generation zeigte Bischofsviolette Blütenfarbe, aber in einer etwas blasseren Nuance, etwa einem Übergang zu Hell Malven (RC 186/1) entsprechend.

Es soll indessen hervorgehoben werden, dass die Nuance der in *V* heterozygoten Individuen nicht in allen Kreuzungen genau gleich stark von den homozygoten, *VV*-Pflanzen abzuweichen scheint. Höchst wahrscheinlich besteht hier noch ein gewisser Einfluss seitens der übrigen genotypischen Konstitution. Vielleicht ist diese Erscheinung von gewissen Kombinationen der Gene für Testafarbe abhängig. Besonders hierauf abzielende Untersuchungen scheinen bisher noch nicht ausgeführt worden zu sein.

In der zweiten Generation der erwähnten Kreuzung Nr. 2, Stella × Wachs Neger, ist folgendes Spaltungsergebnis erhalten worden.

Gefunden: 133 Bischofsviolett-Malven : 41 Laeliafarbig
Erwartet: 130,50 » » : 43,50 »
D/m für 3 : 1 = 0,44

Ferner hat sich herausgestellt, dass die beiden Blütenfarben Bischofsviolett-Malven und Laeliafarbig stets mit ganz bestimmten Testafarben korreliert aufgetreten sind. Gewisse Testafarben kommen also nur mit Bischofsviolett-Malven Blüten, andere dagegen wiederum nur mit Laeliafarbigen vor. Der diesbezüglich gefundene Zusammenhang geht aus der folgenden schematischen Darstellung hervor.

					Testafarbe	Blütenfarbe
F_1: *PPCCJJGgBbVv*	3 *V*	9 *B*	27 *G*	Reinschwarz	Bischofsviolett-Malven
			9 *g*	»	»
		3 *b*	9 *G*	Kastanienbraun	»
			3 *g*	Veilchenviolett	»
	1 *v*	3 *B*	9 *G*	Mineralbraun	Laeliafarbig
			3 *g*	Münzbronze	»
		1 *b*	3 *G*	Bister	»
			1 *g*	Schamois	»

Es stellt sich also heraus, dass sämtliche Individuen mit dem Gen *V* für Testafarbe auch Bischofsviolett-Malvenfarbige Blüten, und diejenigen mit *v* Laeliafarbige Blüten zeigen. Damit erscheint die pleiotrope Wirkung des Gens *V* vollkommen erwiesen. Ausnahmen hiervon haben bisher niemals konstatiert werden können. Die umfangreiche Analyse der dritten und vierten Generation mit über 3000 Individuen hat dies in jeder Hinsicht bestätigt. Diese Resultate zeigen auch, dass die beiden Genpaare *G*—*g* und *B*—*b* keinen okulär ohne weiteres feststellbaren Einfluss auf die Testafarbe zu haben scheinen. Gleiches

scheint auch für die beiden Genpaare *C—c* und *J—j* zu gelten, was in anderen Kreuzungen, Nr. 10 und Nr. 17, bewiesen worden ist. Da von früheren Verfassern (siehe Historik) sowohl für Bischofsviolett—Weiss wie für Laeliafarbig—Weiss monohybride Spaltung im Verhältnis 3 Gefärbt : 1 Weiss gefunden worden ist, müssen hier entweder beide

TABELLE 1. *Die Spaltung der Blütenfarbe in F_2 der Kreuzung Nr. 4: L. 24 aus Merveille du Marché × L. 25 aus Braune Bohne.*

Familien-Nr.	Blüten Bischofsviolett Stamm Rot	Blüten Laeliafarbig Stamm Rosa	Summe Individuen
10331	19	8	27
10332	1	3	4
10333	30	10	40
10334	41	17	58
10335	16	4	20
10336	21	6	27
10337	23	10	33
10338	38	12	50
10339	37	9	46
10340	52	17	69
10341	41	16	57
10342	15	5	20
10343	30	10	40
10344	21	8	29
10345	33	7	40
10346	5	5	10
10347	26	16	42
10348	22	6	28
Summen:	471	169	640
Erwartet:	480,00	160,00	—
D/m für 3 : 1 = ...	0,82	—	—

Eltern Träger des Gens für Laeliafarbige Blüte sein oder es könnte sich auch um eine Spaltung in zwei von drei oder mehreren unilokalen Genen handeln. Darüber soll unten Klarheit erhalten werden.

Eine andere Kreuzung, Nr. 4, wurde ausgeführt zwischen L. 24 aus der Wachsbohnensorte Merveille du Marché und L. 25 aus Braune Bohne. L. 24 hat Bischofsviolette Blüten, L. 25 Laeliafarbige. F_1 hatte gleichwie in Kreuzung Nr. 2 Bischofsviolette Blüten und F_2 zeigte sowohl hinsichtlich Blüten- wie Testafarbe gleiche Spaltung wie die eben genannte Kreuzung. In Kreuzung Nr. 4 wurden die Individuen auch

auf die Stammfarbe untersucht. Die Spaltungsresultate sind in Tabelle i wiedergegeben. Wie aus dieser Tabelle ersichtlich ist, hatten sämtliche Individuen mit Bischofsvioletten Blüten Rote Stammfarbe und die mit Laeliafarbigen Blüten Rosa Stammfarbe.

Die eben erwähnte Beziehung zwischen Blüten- und Stammfarbe hat auch für die früher besprochene Kreuzung Nr. 2 an Individuen der fünften Generation verifiziert werden können. Für Kreuzung Nr. 4 gilt i. ü. alles was oben für Kreuzung Nr. 2 angeführt worden ist.

Die Ergebnisse der beiden vorstehend mitgeteilten Kreuzungen, Nr. 2 und 4, zeigen also, dass *V* in diesen Fällen eine in mehreren Hinsichten ausgeprägte pleiotrope Wirkung hat. Die Wirkung von *V* äussert sich hier in:

1) Bischofsviolette Blütenfarbe,
2) Damit stets gleichzeitig auftretende anthocyanfarbige feine Strichelchen auf Kelchblätter, Vorblätter und Blütenstiel (siehe voriges Kapitel),
3) Rote Stammfarbe, und
4) Bestimmte Testafarbe, je abhängig von der sonstigen genotypischen Konstitution.

Das Gen *V* bei *Phaseolus vulgaris* hat also in gewisser Hinsicht analoge Wirkung wie das Gen *A* bei *Pisum sativum*. Letzteres verursacht bekanntlich Ausbildung von Blütenfarbe und Testafarbe sowie ist Bedingung für das Auftreten von Anthocyanfärbung auf vegetativen Teilen der Pflanze (Ring an der Basis der Nebenblätter etc.).

Zwecks Klarlegung des Verhaltens des Genpaares *V*—*v* zu *P*—*p* und zum Genpaar für das Eigenschaftspaar Laeliafarbige—Weisse Blüten wurden die beiden Elternlinien der vorstehenden Kreuzung Nr. 4 je mit einer dritten Linie gekreuzt, von der bekannt war, dass sie sich in wenigstens zwei dieser Genpaare unterschied. Gewählt wurde hierzu Linie 28 aus der schwedischen Schwertbohnensorte Favorit der Firma W. Weibull, Landskrona. In bezug auf diese Linie war auf Grund von Kreuzungsresultaten (siehe LAMPRECHT 1932 c, Kreuzung Nr. 5) bekannt, dass ihr die Genenformel *pp cc JJ gg BB vv* zukommt. Ausserdem hat sie Weisse Blütenfarbe. Ob L. 28 Träger des Gens für Laeliafarbige Blüte war, konnte natürlich nicht entschieden werden, da sie in ihrer Formel *p*, also das Grundgen für die Ausbildung von Testa- und Blütenfarbe in rezessiver Form hatte.

Die eine der beiden Kreuzungen, Nr. 16, wurde also ausgeführt zwischen L. 24 aus der Wachsbohne Merveille du Marché mit Bischofsvioletten Blüten und L. 28 aus Favorit mit Weissen Blüten. Die Indi-

TABELLE 2. *Die Spaltung der Blütenfarbe in F_2 der Kreuzung Nr. 16: L. 24 aus Merveille du Marché × L. 28 aus Favorit.*

Familien-Nr.	Blüten Bischofsviolett	Blüten Weiss	Summe Individuen
10741	16	16	32
10742	18	11	29
10743	2	4	6
10744	14	4	18
10745	4	4	8
10746	17	16	33
10747	18	27	45
10748	20	19	39
10749	1	—	1
10750	13	7	20
10751	25	9	34
10752	—	1	1
10753	11	8	19
10754	6	12	18
10755	22	11	33
10756	31	25	56
10757	8	10	18
10758	22	17	39
10759	18	27	45
10760	17	21	38
10761	19	16	35
10762	29	31	60
10763	41	35	76
10764	11	9	20
10765	68	57	125
10766	21	16	37
10767	27	25	52
10768	20	22	42
10769	72	17	89
10770	5	—	5
10771	33	29	62
10772	30	12	42
10773	3	4	7
10774	19	9	28
10775	22	18	40
10776	41	23	64
10777	23	27	50
10778	42	36	78
10779	19	12	31
10780	6	6	12
10781	7	5	12
10782	13	16	29
10783	29	24	53
10784	25	12	37
10785	30	18	48
10786	45	21	66
10787	33	28	61
Summen:	1016	777	1793
Erwartet:	1008,56	784,44	—
D/m für 9:7 = ...	0,36	—	—

viduen der ersten Generation zeigten Bischofsviolette Blüten, aber von etwas blasserer Nuance als L. 24, was auf Heterozygotie zurückzuführen ist. Letzteres ist, wie in der Historik erwähnt worden ist, bereits von TJEBBES und KOOIMAN (1921) und PRAKKEN (1934) nachgewiesen worden.

Die in der zweiten Generation erhaltenen Spaltungsresultate sind in Tabelle 2 mitgeteilt. Wie aus dieser ersichtlich ist, wurde eine Spaltung in nur zwei Blütenfarben, nämlich Bischofsviolett und Weiss erhalten. Die gefundenen Spaltungszahlen sprechen für eine klare dihybride Spaltung im Verhältnis 9 Bischofsviolett : 7 Weiss mit $D/m = 0{,}36$, also sehr gute Übereinstimmung mit dem theoretischen Verhältnis anzeigend.

Dieses Spaltungsergebnis ist jedoch in gewisser Hinsicht überraschend. Dass $^{7}/_{16}$ der Individuen Weisse Blüten haben war zu erwarten, denn die beiden Elternlinien unterscheiden sich sowohl im Genpaar *P—p* wie *V—v*. Aber Linie 24 sollte — wenn es sich hier nicht um eine Spaltung in unilokale Faktoren handelt — überdies Träger des Gens für Laeliafarbige Blüten sein, denn in Kreuzung Nr. 4 führte diese Linie nach Befruchtung mit L. 25 mit Laeliafarbigen Blüten zu einer monohybriden Aufspaltung im Verhältnis 3 Bischofsviolett : 1 Laeliafarbig. Und solchenfalls sollten in vorliegender Kreuzung, Nr. 16, auch Individuen mit Laeliafarbigen Blüten aufgetreten sein. Schon dies macht — wenn es sich nicht um unbekannte, komplizierte Verhältnisse handelt — die Annahme wahrscheinlich, dass die drei Blütenfarben Bischofsviolett—Laeliafarbig—Weiss durch drei unilokale Faktoren bedingt werden. Eine klare Antwort hierauf wird durch die folgende Kreuzung, Nr. 10, erhalten.

Kreuzung Nr. 10 wurde ausgeführt zwischen L. 25 mit Laeliafarbigen Blüten und L. 28 mit Weissen Blüten. Die genotypische Konstitution für L. 25 ist *PP CC JJ GG bb vv*, die für L. 28 *pp cc JJ gg BB vv*. L. 25 hat Laeliafarbige, L. 28 Weisse Blüten. Die Individuen der F_1-Generation von Kreuzung Nr. 10 zeigten Laeliafarbige Blüten. F_2 zeigte folgende Spaltung:

Gefunden: 1818 Laeliafarbig : 1318 Weiss
Erwartet: 1764,0 » : 1372,0 »
D/m für 9 : 7 = 1,94

Zweifellos liegt hier eine dihybride Spaltung vor, an der teils das Genpaar *P—p*, teils das Genpaar für Laeliafarbige—Weisse Blüten beteiligt sind. Damit ist auch einwandfrei bewiesen, dass für die drei Blüten-

farben Bischofsviolett, Laeliafarbig und Weiss, drei unilokale Gene (multiple Allelen) verantwortlich sind, denn lässt man die Spaltung im Grundgen für die Ausbildung von Farbe *P—p* (in den zwei Kreuzungen Nr. 10 und 16) weg, so spalten die drei Kreuzungen je im monohybriden Verhältnis 3 : 1. Hierbei dominiert die dunklere Blütenfarbe stets über die hellere, also Bischofsviolett über Laeliafarbig und Laeliafarbig über

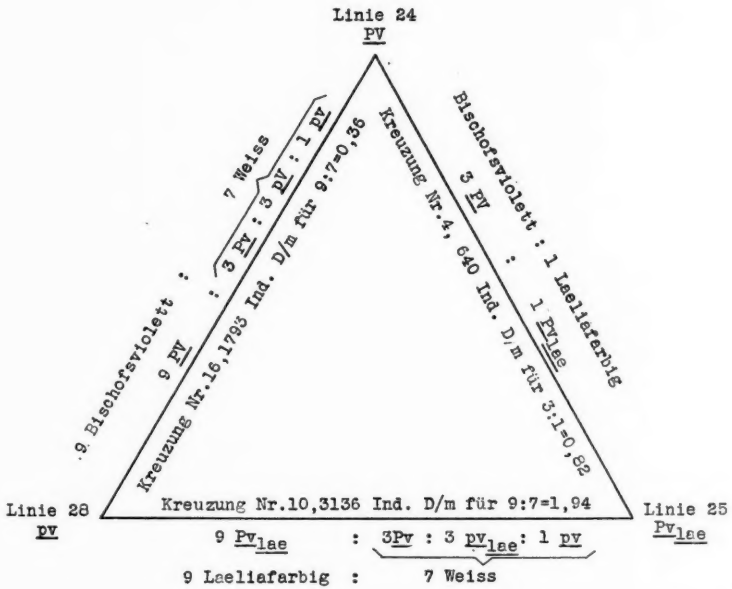
Linie 24
PV
Kreuzung Nr.4, 640 Ind. D/m für 3:1=0,82
3 PV : 1 Pvlae
Bischofsviolett : 1 Laeliafarbig
Kreuzung Nr.16,1793 Ind. D/m für 9:7=0,36
9 PV : 3 PV : 3 pv : 1 pv
9 Bischofsviolett : 7 Weiss
Linie 28
pv
Kreuzung Nr.10,3136 Ind. D/m für 9:7=1,94
Linie 25
Pvlae
9 Pvlae : 3Pv : 3 pvlae : 1 pv
9 Laeliafarbig : 7 Weiss

Fig. 2. Schematische Darstellung der Kreuzungsresultate zwischen den drei Linien Nr. 24, 25 und 28, die Spaltung in den drei unilokalen Genen $V—v_{lae}—v$ veranschaulichend. Zwei der Kreuzungen sind überdies durch gleichzeitige Spaltung im Genpaar *P—p* kompliziert.

Weiss. Und die drei Kreuzungen wurden mit drei reinen Linien — diesen drei Blütenfarben entsprechend — als Eltern ausgeführt.

Eine instruktive Übersicht über die Spaltungen dieser drei Kreuzungen gibt die in Fig. 2 wiedergegebene schematische Darstellung. Das für die Ausbildung von Laeliafarbig verantwortliche Gen bezeichne ich mit v_{lae}, wobei der Index zu *v* von *laeliacoloratus* = Laeliafarbig abgeleitet ist. Für die drei in vorstehenden Kreuzungen untersuchten Blütenfarben erhalten wir demnach:

V = Bischofsviolett
v_{lae} = Laeliafarbig
v = Weiss

Hier sei erwähnt, dass mir wenigstens noch eine weitere Blütenfarbe, mit einer blasseren, etwas ins Rosa gehenden Nuance als Laeliafarbig, bekannt ist. Eine Kreuzung, ausgeführt zwischen einer Linie mit dieser Blütenfarbe und einer Linie mit *PP vv* hat in F_2 monohybride Spaltung im Verhältnis 3 Gefärbt : 1 Weiss ergeben. Es erscheint demnach sehr wahrscheinlich, dass wir es mit noch einem weiteren unilokalen Gen für Blütenfarbe zu tun haben. Bevor aber die Zugehörigkeit des betreffenden Gens zur in Rede stehenden Serie von unilokalen Genen sicher bewiesen ist, will ich von einer Benennung desselben absehen.

Aus der recht beträchtlichen Serie von Kreuzungen (über 50), die von mir während den Jahren 1928—1934 mit Hinsicht auf die Vererbung der Blütenfarbe untersucht worden sind, teile ich hier zuerst einige mit, die das Verhältnis der oben besprochenen drei unilokalen Gene zum Grundgen *P*, zum Gen für Totalfärbung der Testa *T* (bzw. *E*) und zur Stammfarbe beleuchten.

Kreuzung Nr. 18, über die in bezug auf Spaltung in Testafarben früher (LAMPRECHT 1933) ausführlich berichtet worden ist, wurde ausgeführt zwischen L. 33 aus l'Inepuisable mit Weissen Blüten und L. 35 aus der Wachsbohne Hundert für Eine mit Laeliafarbigen Blüten. Die F_1-Generation zeigte in dieser Kreuzung Bischofsviolette Blüten, was bei Kenntnis der Formeln für die Testafarbe auch zu erwarten gewesen ist. L. 33 hat die Formel: *pp cc JJ GG BB VV*, L. 35: *PP CC JJ GG bb vv*. Da L. 35 aber Laeliafarbige Blüten hat, ist in ihrer Formel — mit Hinblick auf die oben gewonnenen Kenntnisse — *vv* durch v_{lae} v_{lae} zu ersetzen. Falls *pp* die Wirkung von *V* und v_{lae} auf die Blütenfarbe inhibiert — wofür alle bisherigen Resultate sprechen — ist in F_2 eine Spaltung im Verhältnis 9 Bischofsviolett : 3 Laeliafarbig : 4 Weiss zu erwarten.

Tabelle 3, in der die Ergebnisse der Analyse der F_2-Generation mitgeteilt sind, bestätigt diese Erwartung. Es besteht geradezu ausgezeichnete Übereinstimmung zwischen den gefundenen Zahlen und den theoretisch erwarteten. Ausserdem zeigt die Tabelle, dass die drei Stammfarben Rot, Rosa und Grün den drei Blütenfarben Bischofsviolett, Laeliafarbig und Weiss entsprechen, demnach mit den drei unilokalen Genen *V*, v_{lae} und *v* parallel gehen. Das Grundgen *P* in seiner rezessiven Form (*p*) verhindert also auch die Ausbildung von sowohl Roter wie Rosa Stammfarbe.

Die nächste hier zu besprechende Kreuzung, Nr. 89, wurde ausgeführt zwischen L. 5 aus der französischen Brechbohnensorte Incom-

TABELLE 3. *Die Spaltung in bezug auf Blüten- und Stammfarbe in F_2 der Kreuzung Nr. 18: L. 33 aus l'Inepuisable × L. 35 aus Hundert für Eine Wachs.*

Familien-Nr.	Blüten Bischofsviolett Stamm Rot	Blüten Laeliafarbig Stamm Rosa	Blüten Weiss Stamm Grün	Summe Individuen
11141	48	13	18	79
11142	34	17	20	71
11143	22	10	6	38
11144	60	23	19	102
11145	59	25	17	101
11146	27	7	8	42
11147	41	10	30	81
11148	50	20	32	102
11149	49	19	18	86
11150	57	8	11	76
11151	25	6	15	46
11152	28	8	17	53
11153	52	16	22	90
11154	28	15	10	53
11155	27	12	10	49
11156	44	10	19	73
11157	36	18	15	69
11158	27	14	16	57
11159	33	11	16	60
11160	25	15	15	55
11161	29	5	11	45
11162	36	7	19	62
11163	36	9	18	63
11164	51	17	20	88
11165	27	4	14	45
Summen:.....	951	319	416	1686
Erwartet:.....	948,375	316,125	421,50	—
D/m für 9:3:4 = ...	0,13	0,18	0,31	—

parable und L. 20 aus der amerikanischen Brechbohnensorte Navy. Beide Linien haben Weisse Blütenfarbe. L. 5 hat teilfarbige Samen vom *bipunctata*-Typus (siehe LAMPRECHT 1934). Von ihrer genotypischen Konstitution kommen hier folgende Gene in Betracht: *PP tt VV*. L. 20 hat weisse Testafarbe und folgende Konstitution: *pp TT VV*. Das

Gen *T* ist für die Ganzfarbigkeit der Testa erforderlich. Laut EMERSON (1904) sollten teilfarbige Bohnensorten »meistens» Weisse Blütenfarbe haben. Die vorliegende Kreuzung wird demnach gestatten zu entscheiden in welchem Masse dies richtig ist.

Die erste Generation dieser Kreuzung hatte Bischofsviolette Blüten. Da beide Elternlinien Weisse Blüten hatten, und überdies das Gen *V*

TABELLE 4. *Die Spaltung der Blütenfarbe in F_2 der Kreuzung Nr. 89: L. 5 aus Incomparable × L. 20 aus Navy.*

Familien-Nr.	Blüten Bischofsviolett	Blüten Weiss	Summe Individuen
4107	85	85	170
4108	53	45	98
4109	124	86	210
Summen:	262	216	478
Erwartet:	268,87	209,13	—
D/m für 9:7 = ...	0,63	—	—

enthielten (konstatiert auf Grund der Testafarbenspaltung), muss in jeder dieser Linien die Ausbildung von Blütenfarbe durch ein Grundgen verhindert worden sein. Im einen Falle (L. 20) war dies das Grundgen *p* für die Ausbildung von Testa- und Blütenfarbe, im anderen war es das Gen *t* für Teilfarbigkeit der Testa. Anwesenheit von *T* in dominanter Form ist demnach Bedingung für die Ausbildung von Blütenfarbe. Für die Ausbildung von Blütenfarbe bestehen demnach zwei Grundgene: *P* und *T*.

In der zweiten Generation ist also eine dihybride Spaltung im Verhältnis 9 Gefärbt : 7 Weiss zu erwarten. Die erhaltenen Resultate, die in Tabelle 4 zusammengestellt sind, bestätigen dies. Die gefundenen Spaltungszahlen stimmen gut mit den theoretisch erwarteten überein. Und die weissblütigen Individuen hatten stets entweder Reinweisse oder teilfarbige Samen. Unter den Individuen mit Bischofsvioletten Blüten gab es keine, die solche Samen produzierten.

Im Anschluss an die Feststellung, dass in Kreuzung Nr. 89 alle ausspaltenden Individuen mit teilfarbigen Samen auch Weisse Blütenfarbe zeigten, sei erwähnt, dass diese Erscheinung von mir in einer Reihe von Kreuzungen ausnahmslos hat bestätigt werden können. Auch wenn die Ausbreitung der Farbe auf der Testa bei teilfarbigen Typen eine sehr grosse gewesen ist, d. h. wenn also nur wenige weisse Punkte am einen Ende wahrzunehmen waren (vgl. LAMPRECHT 1934, S. 192, *minimus-*

Typus), ist die Blütenfarbe Weiss gewesen. Gleiches gilt für sämtliche untersuchten Linien und spontanen Kreuzungen. Dies verdient vielleicht hervorgehoben zu werden, da EMERSON (1904) schreibt: »Where seeds are white with but a small amount of color about the eye, the flowers are also sometimes white».

TABELLE 5. *F_2 der Kreuzung Nr. 27: L. 33 aus l'Inepuisable × L. 45 sellatus-Typus.*

Familien-Nr.	Blüten Bischofsviolett Stamm Rot	Blüten Laeliafarbig Stamm Rosa	Blüten Weiss Stamm Grün	Summe Individuen
3661	28	11	51	90
3662	24	9	16	49
3663	13	4	16	33
3664	32	8	25	65
3665	42	16	38	96
3666	41	12	33	86
3667	12	3	14	29
8652	27	10	23	60
8653	36	10	43	89
8654	27	3	26	56
8655	13	2	9	24
8656	18	4	10	32
8657	45	9	46	100
8658	43	11	26	80
8659	52	10	22	84
Summen:.....	453	122	398	973
Erwartet:.....	410,48	136,83	425,69	—
D/m für 27:9:28..=	2,76	1,37	1,79	—

Eine weitere Kreuzung, Nr. 27, wurde ausgeführt zwischen der bereits erwähnten Linie 33 aus l'Inepuisable und Linie 45, einer Brechbohne mit teilfarbigen Samen vom *sellatus*-Typus (siehe LAMPRECHT 1934). Beide Linien haben Weisse Blütenfarbe und Grüne Stammfarbe. L. 33 kommt die genotypische Formel *pp TT cc JJ GG BB VV* zu, L. 45 *PP tt CC JJ GG bb*. Ob L. 45 v_{lae} oder *v* enthält, müssen erst die Kreuzungsresultate entscheiden.

In bezug auf das Genpaar *T—t* sei hier unter Hinweis auf eine frühere Arbeit (LAMPRECHT 1934) hervorgehoben, dass es sich — da für die Ausbildung von Teilfarbigkeit die beiden Genpaare *T—t* und *E—e* verantwortlich sind — um ein beliebiges dieser handeln kann; denn

diese beiden Genpaare haben in ihrer Wirkung bisher nicht voneinander unterschieden werden können.

Die Individuen der F_1-Generation zeigten Bischofsviolette Blüten- und Rote Stammfarbe. Die in F_2 erhaltenen Spaltungsresultate sind in Tabelle 5 mitgeteilt. Als Resultat gibt diese Tabelle eine Spaltung im Verhältnis 27 Bischofsviolett : 9 Laeliafarbig : 28 Weiss, also eine trihybride Spaltung an. L. 45, die eine Elternlinie, hat demnach v_{tae} in ihrer Konstitution. Eine schematische Übersicht über die hier in Frage kommenden, spaltenden Genpaare ergibt sogleich, dass gerade diese Spaltung zu erwarten gewesen ist.

$$Pp\ Tt\ Vv_{tae} \xrightarrow{F_1} \begin{cases} 48\ P \begin{cases} 36\ T \begin{cases} 27\ V \text{ Bischofsviolett} \\ 9\ v_{tae} \text{ Laeliafarbig} \end{cases} \\ 12\ t \ldots \end{cases} \\ 16\ p \ldots\ldots\ldots \end{cases} 28\ p + t \text{ Weiss}$$

TABELLE 6. *F_2 der Kreuzung Nr. 34: L. 33 aus l'Inepuisable $\times$ L. 10 sellatus-Typus.*

Familien-Nr.	Blüten Bischofsviolett Stamm Rot	Blüten Weiss		Summe Individuen
		Stamm Rosa	Stamm Grün	
8558	28	5	19	52
8559	34	17	41	92
8560	47	18	50	115
8561	17	6	17	40
8562	32	9	44	85
8563	49	19	54	122
8564	31	8	33	72
8565	75	11	55	141
8566	62	23	59	144
8567	18	5	17	40
Summen:	393	121	389	903
Erwartet:	380,95	126,98	395,07	—
D/m für 27 : 9 : 28 .. =	0,81	0,57	0,41	—

Die Stammfarbe geht hier, gleichwie bereits früher in Kreuzung Nr. 18, Tab. 3, festgestellt worden ist, mit den Blütenfarben parallel, indem Bischofsviolett mit Roter Stammfarbe, Laeliafarbig mit Rosa Stammfarbe und Weiss mit Grüner Stammfarbe stets gemeinsam auftritt. Die Resultate der vorliegenden Kreuzung gestatten demnach den Schlusssatz, dass auch die Ausbildung von Stammfarbe von der Anwesenheit der beiden Gene *P* und *T* in dominanter Form abhängig ist.

Die nächste zu besprechende Kreuzung, Nr. 34, wurde ausgeführt zwischen der einen Elternlinie der eben besprochenen Kreuzung, L. 33, und einer Schwesterlinie zu L. 45, nämlich L. 10. Letztere war — okulär betrachtet — ganz mit L. 45 übereinstimmend. Sie hatte also u. a. gleichwie diese Weisse Blüten und teilfarbige Samen vom *sellatus*-Typus. Auch in dieser Kreuzung zeigten die F_1-Individuen Bischofsviolette Blütenfarbe und Rote Stammfarbe. Aber die Spaltung in F_2 war nicht dieselbe, wie die in der eben besprochenen Kreuzung Nr. 27. Es sind keine Individuen mit Laeliafarbigen Blüten aufgetreten. Die Spaltungszahlen sind in Tabelle 6 zusammengestellt.

Aus den Resultaten in Tab. 6 ergibt sich, dass die eine Elternlinie, L. 10, nicht wie ihre Schwesterlinie, L. 45, v_{lae} sondern v in ihrer Konstitution hat. Eine schematische Darstellung der hier spaltenden Genpaare führt dann zu folgendem Bild.

$$F_1\text{: } Pp\ Tt\ Vv \ldots \begin{cases} 48\ P \begin{cases} 36\ T \begin{cases} 27\ V \text{ Bischofsviolett} \\ 9\ v \end{cases} \\ 12\ t \ldots\ldots \end{cases} \\ 16\ p \ldots\ldots\ldots\ldots \end{cases} 37 \text{ Weiss}$$

Wir hätten also gerade die gefundene Spaltung 27 Bischofsviolett : 37 Weiss zu erwarten. Ohne Kenntnis der dieser Kreuzung zugrunde liegenden Genpaare würde man gerne geneigt sein, diese Spaltung als dem dihybriden Verhältnisse 7 Bischofsviolett : 9 Weiss entsprechend aufzufassen. Die gefundenen Zahlen stimmen nämlich mit den hierfür theoretisch zu erwartenden sehr gut überein. D/m erreicht hierfür den Wert von nur 0,14!

Verbleibt eine Erklärung der in bezug auf die Stammfarbe gefundenen Spaltung. Hier besteht nicht, wie man erwartet hätte, Korrelation zwischen Rosa Stammfarbe und Laeliafarbigen Blüten. Letztere Blütenfarbe tritt in dieser Kreuzung überhaupt nicht auf. Aber die Weissblütigen Individuen spalten in bezug auf Stammfarbe im Verhältnis 3 Grün : 1 Rosa. Ist die Rosa Stammfarbe hier durch das Gen v_{lae} bedingt, so würde dies bedeuten, dass die Wirkung dieses Gens auf die Blütenfarbe — Ausbildung von Laeliafarbig — in der vorliegenden Kreuzung durch ein anderes (oder mehrere andere) Gene unterdrückt wird. Es besteht aber auch eine andere, vielleicht wahrscheinlichere Erklärungsmöglichkeit, nämlich die, dass wir es hier mit einem anderen, weiteren unilokalen Gen der vorhin besprochenen Blütenfarbenserie zu tun haben, dass solchenfalls keine Blütenfärbung aber wohl Rosa Stammfarbe verursachen sollte. Wie dem auch sei, so sind dies nur

Annahmen zur Erklärung der gefundenen Erscheinung, die wohl als Arbeitshypothesen verwendet, im übrigen aber erst bewiesen werden müssen.

Im Zusammenhang hiermit ist es von Interesse auf die von MIYAKE, IMAI and TABUCHI (1930) gefundenen Ergebnisse hinzuweisen, nach denen Rote Stammfarbe stets mit Bischofsvioletten Blüten und Rosa Stammfarbe stets mit Laeliafarbigen Blüten einhergeht. Grüne Stammfarbe soll jedoch mit einer beliebigen dieser Blütenfarben sowie mit Weiss und Gestrichelt kombiniert auftreten können. Oben haben wir eine Durchbrechung dieser Regel feststellen können, indem Rosa Stammfarbe mit Weisser Blütenfarbe kombiniert aufgetreten ist. Sicher scheint demnach zu sein, dass Rosa Stammfarbe ausser durch das Gen v_{lae} auch noch durch ein anderes bedingt sein kann.

Bohnenrassen mit einer ausgeprägten Farbenverstärkung am oberen Rand der Fahne, von mir als Terminalverstärkung bezeichnet, scheinen in der genetischen Literatur nicht erwähnt und bisher auch nicht zum Gegenstand einer genetischen Analyse gemacht worden zu sein. Dies trotzdem es im Handel mehrere Sorten mit solchen Blüten gibt. Zwei solche Sorten, aus denen Linien zu den folgenden beiden Kreuzungen verwendet worden sind, sind die deutsche frühe Brechbohnensorte Hinrichs Riesen und die französische Brechbohnensorte Coco marbré.

Die folgende Kreuzung, Nr. 13, wurde ausgeführt zwischen Linie 32 aus Coco marbré und Linie 31 aus der englischen Wachsbohnensorte Centenary Gold Podded. L. 32 hat in ihrer genotypischen Konstitution, soweit sie hier in Frage kommt, *PP TT* $v_{lae}v_{lae}$ sowie Terminalverstärkung der Fahnenfarbe. Die Samen dieser Linie sind also ganzfarbig. L. 31 hat in ihrer genotypischen Konstitution *PP tt VV* sowie keine Terminalverstärkung der Fahnenfarbe. L. 32 hat demnach Laeliafarbige Blüten mit Terminalverstärkung, L. 31 Weisse Blüten, da sich *VV* auf Grund von *tt* nicht geltend machen kann.

Die Individuen der ersten Generation zeigten Bischofsviolette Blüten mit Terminalverstärkung, so wie diese im vorigen Kapitel beschrieben worden sind, und ferner ganzfarbige Samen. Es kann mithin festgestellt werden, dass die Terminalverstärkung eine dominante Erscheinung ist. Wenn die genotypische Grundlage für die Ausbildung von Terminalverstärkung nur bei Anwesenheit der beiden Grundgene für Blütenfarbe, *P* und *T*, sich geltend machen kann, so haben wir in der zweiten Generation eine Aufspaltung in teils Weisse Blüten, auf Grund von Heterozygotie in *Tt*, teils Bischofsviolette und

TABELLE 7. *Die Spaltung in bezug auf Blütenfarben in F_2 von Kreuzung Nr. 13: L. 31 aus Centenary Gold Podded × L. 32 aus Coco marbré.*

Familien-Nr.	Blüten Bischofsviolett		Blüten Laeliafarbig		Blüten Weiss	Summe Individuen
	mit Terminalverstärkung	ohne Terminalverstärkung	mit Terminalverstärkung	ohne Terminalverstärkung		
11041	13	5	8	2	2	30
11042	5	2	1	2	9	19
11043	3	—	1	—	—	4
11044	2	1	2	1	1	7
11045	17	6	8	—	7	38
11046	4	4	1	—	—	9
11047	3	4	2	—	2	11
11048	3	3	1	4	1	12
11049	6	1	3	1	5	16
11050	6	5	1	—	1	13
11051	14	4	5	1	3	27
11052	3	4	3	1	4	15
11053	5	3	5	—	5	18
11054	10	3	11	2	9	35
11055	8	4	3	2	6	23
11056	7	10	4	—	9	30
11057	4	1	2	—	2	9
11058	6	1	3	—	2	12
11059	17	2	5	—	14	38
11060	14	2	4	—	10	30
11061	18	1	4	1	15	39
11062	6	3	1	—	5	15
11063	6	1	2	1	6	16
11064	16	9	2	—	9	36
11065	7	3	1	—	4	15
11066	7	2	2	—	5	16
11067	11	4	2	—	4	21
11068	8	2	—	—	9	19
11069	8	3	—	3	3	17
11070	19	4	4	—	7	34
11071	9	4	—	—	7	20
11072	7	2	5	—	3	17
11073	15	5	2	3	10	35
11074	7	—	—	—	—	7
11075	12	5	1	2	7	27
11076	1	—	1	—	—	2
11077	7	3	3	1	4	18
11078	8	1	1	3	3	16
11079	10	4	5	—	8	27
11080	4	1	—	1	2	8
11081	3	1	1	—	5	10
11082	18	5	3	1	6	33
11083	12	3	2	1	5	23
11084	12	3	1	2	6	24
11085	8	6	3	4	10	31
11086	8	1	—	—	4	13
Summen:	397	141	119	39	239	935
Erwartet:	394,45	131,48	131,48	43,83	233,75	—
D/m für 27 : 9 : 9 : 3 : 16 =	0,17	0,90	1,18	0,77	0,40	—

Laeliafarbige Blüten sowohl mit wie ohne Terminalverstärkung zu erwarten. Dies ist auch tatsächlich eingetroffen. Die Ergebnisse der F_2-Analyse sind in Tabelle 7 wiedergegeben.

Aus der Tabelle ist vor allem ersichtlich, dass eine Spaltung in Individuen mit Gefärbten und Weissen Blüten stattgefunden hat, bedingt durch das Genpaar *T—t*. Diese Spaltung ist monohybrid im Ver-

TABELLE 8. *Die Spaltung der Blütenfarbe in F_2 der Kreuzung Nr. 133: L. 62 aus einer afrikanischen Sorte × L. 130 aus Hinrichs Riesen.*

Familien-Nr.	Blüten Laeliafarbig		Summe Individuen
	mit Terminalverstärkung	ohne Terminalverstärkung	
4188	48	9	57
4189	31	6	37
4190	15	2	17
4191	21	2	23
4192	16	5	21
4193	16	6	22
4194	11	6	17
4195	18	21	39
4196	12	18	30
4197	19	18	37
4198	19	20	39
4199	13	12	25
4200	10	19	29
4201	16	27	43
4202	6	9	15
4203	10	29	39
4204	25	33	58
Summen:	306	242	548
Erwartet:	308,25	239,75	—
D/m für 9:7 = ...	0,19	—	—

hältnis 3 : 1 mit D/m = 0,40. Sämtliche Weissblütigen Individuen haben auch teilfarbige Samen (*tt*) gehabt. Die Gefärbtblütigen spalten im Verhältnis 9 Bischofsviolett mit Terminalverstärkung : 3 Bischofsviolett ohne Terminalverstärkung : 3 Laeliafarbig mit Terminalverstärkung : 1 Laeliafarbig ohne Terminalverstärkung. Im ganzen resultiert daher das unten in der Tabelle 7 angeführte Spaltungsverhältnis 27 : 9 : 9 : 3 : 16. Ganz zweifellos haben wir es hier mit einer Spaltung in den zwei Genpaaren *T—t* und *V—v_{lae}* sowie in einem weiteren Genpaar, das die Terminalverstärkung bedingt, zu tun.

Letzteres Genpaar will ich, mit Hinblick auf die Wirkung der rezessiven Form desselben, mit dem Symbol *Aeq—aeq* bezeichnen, hergeleitet von *aequicoloratus* = gleichmässig gefärbt, im Gegensatz zur dominanten Form: mit Terminalverstärkung.

Da die in Kreuzung Nr. 13 gefundenen Spaltungszahlen durchweg befriedigende Übereinstimmung mit den theoretisch erwarteten aufweisen, die Werte für D/m variieren zwischen 0,17 und 1,18, erscheint es sehr wahrscheinlich, dass die drei Genpaare *T—t*, *V—v_{lae}* und *Aeq—aeq* unabhängig voneinander vererbt werden.

Schliesslich seien hier die Resultate einer Kreuzung mitgeteilt, die zeigen, dass die Terminalverstärkung durch das Zusammenwirken von zwei Genen bedingt wird. Die in Frage stehende Kreuzung, Nr. 133, wurde ausgeführt zwischen Linie 62 und Linie 130. L. 62 ist eine niedrige Brechbohnensorte mit Schamoisfarbigen grossen Samen, die im Mount Kenia-Gebiet in Ostafrika von den Eingeborenen gebaut wird und von der Samen vom Afrika-Forscher H. GRANVIK nach Schweden mitgebracht worden sind. L. 130 ist eine Linie aus der bekannten deutschen Brechbohnensorte Hinrichs Riesen; diese Linie zeichnet sich u. a. durch besonders grosse Vorblätter aus. L. 62 hat Laeliafarbige Blüten, L. 130 gleichfalls aber mit Terminalverstärkung.

Die Individuen der ersten Generation dieser Kreuzung zeigten Laeliafarbige Blüten mit Terminalverstärkung. Die in F_2 erhaltenen Spaltungsresultate sind in Tabelle 8 wiedergegeben und zeigen gute Übereinstimmung mit einer dihybriden Spaltung im Verhältnisse 9 Laeliafarbig mit Terminalverstärkung : 7 Laeliafarbig. Für die Ausbildung der Terminalverstärkung auf der Fahne der Bohnenblüte scheint demnach ausser das Gen *Aeq* noch ein zweites, auf seine ev. sonstige Wirkung noch nicht untersuchtes Gen verantwortlich zu sein.

Ein Rückblick auf die in vorliegender Arbeit mitgeteilten Kreuzungsresultate ergibt, dass die Vererbung der Blütenfarben bei *Phaseolus vulgaris* in ihrer Gänze von recht komplizierter Natur ist. Eine Kombination z. B. des trihybriden Spaltungstypus in Kreuzung Nr. 34 mit Spaltung hinsichtlich Terminalverstärkung nach dem oben mitgeteilten dihybriden Schema führt zu einem pentahybriden Spaltungstypus (aber mit nur 4 spaltenden Blütenfarben), der ohne eingehende Kenntnis der beteiligten Genpaare und ihrer gegenseitigen Wirkungsweise äusserst schwer erklärbar erscheinen dürfte. Schon zu Beginn meiner genetischen Untersuchungen von *Phaseolus vulgaris* bin ich auf solche Spaltungstypen gestossen, die erst jetzt ihrer Lösung entgegengehen. In solchen Kreuzungen sind auch Weissblütige Individuen (mit

P und *T*) mit Terminalverstärkung ausgespalten, ein Typus, von dem kurz darauf auch eine Sorte im Handel erschienen ist; es ist dies die französische Brechbohnensorte d'Eyragues. Über die Ergebnisse solcher Kreuzungen sowie über die Vererbung der Stammfarben im Verhältnis zu den Blütenfarben und weiteren Typen von Blütenfarben hoffe ich in nächster Zeit berichten zu können.

Auf Grund der in dieser Arbeit mitgeteilten und schon früher von anderen Forschern veröffentlichten Resultate können die genetischen Grundlagen für die Ausbildung und Vererbung der Blütenfarben von *Phaseolus vulgaris* etwa folgendermassen zusammengefasst werden.

Grundbedingung dafür, dass es überhaupt zur Ausbildung von gefärbten Blüten kommen können soll, ist Anwesenheit in dominanter Form des Grundgens für die Ausbildung von Testafarbe, *P*, sowie des Gens für die Ausbildung von ganzfarbiger Testa, *T* (bzw. *E*). Diese Gene fungieren demnach als Grundgene für die Ausbildung von Blütenfarbe. Individuen mit *p* oder *t* haben also stets Weisse Blüten. Überdies ist für die Ausbildung von gefärbten Blüten noch die Anwesenheit eines der Gene *V* oder v_{lae} der drei unilokalen Gene $V—v_{lae}—v$ erforderlich. Blüten mit *v* sind also auch stets Weiss. Es besteht wenigstens noch ein weiteres Gen für eine sehr blasse Blütenfarbe, das wahrscheinlich auch zur Reihe der unilokalen Gene gehören dürfte. *V* verursacht Bischofsviolette, v_{lae} Laeliafarbige Blüten.

Da *V* zusammen mit *P* und anderen Genen gewisse Testafarben verursacht, besteht in dieser Hinsicht ein bestimmter Zusammenhang zwischen Blüten- und Testafarbe. Von den übrigen fünf Farbgenen für Testafarbe haben aber *C*, *J*, *G* und *B* (*R* ist noch zu wenig untersucht) keinerlei Einfluss auf die Blütenfarbe gezeigt. Es sind daher ohne weiteres Rassen mit farbigen Samen und Weissen Blüten erhältlich. Da ferner v_{lae} keinen Einfluss auf die Testafarbe hat, ist auch das Umgekehrte realisierbar, d. h. Rassen mit Laeliafarbigen Blüten und Weissen Samen. Solchen Rassen müssen natürlich die Gene für Testafarbe fehlen.

SHAW und NORTONS (1908) Äusserung, dass die spärlichen Angaben über das Vorkommen von weisssamigen Rassen mit gefärbten Blüten wahrscheinlich Irrtümer sind, muss also die Berechtigung aberkannt werden. Und dasselbe gilt für EMERSONS (1904) Behauptung: »The darker the seeds, the darker the flowers». Dieser Auffassung könnte nur insofern beigepflichtet werden, als in den Fällen wo durch das

Hinzukommen von *V* eine dunklere Samenfarbe hervorgerufen wird, gleichzeitig auch eine dunklere Blütenfarbe, Bischofsviolett, auftritt. Auf der anderen Seite haben wir aber die ganze lange Reihe von Testafarben, von hellsten bis zu dunklen Farben, verursacht durch verschiedene Kombinationen der übrigen Gene für die Testafarbe. Und diese sind ohne jede Wirkung auf die Blütenfarbe.

Ausser den eben besprochenen Genpaaren für die Ausbildung von Blütenfarben sind bisher noch drei weitere bekannt, die die beiden Blütenfarben Bischofsviolett und Laeliafarbig in bestimmter Weise verändern.

SHAW (1913) konstatierte das Vorhandensein eines Gens, das in dominanter Form Bischofsviolett in crimson (Purpur) verwandelt und zugleich Purpurfärbung von Blättern und Stamm verursacht. Laeliafarbig wird durch dieses Gen in waxy pink (siehe Historik) verwandelt und ausserdem bekommen Blätter und Stamm ein wachsig—bräunlichgelbes Aussehen. Das hierfür verantwortliche Genpaar will ich mit dem Symbol *Nud—nud* bezeichnen, abgeleitet von *nudus* = nackt, der rezessiven Eigenschaft — ohne wachsigen oder purpurnen Überzug — entsprechend. Eine SHAWs crimson-Typus entsprechende Bohnenrasse habe ich aus Botanischen Gärten unter der Bezeichnung *Phaseolus glaber* erhalten, und gegenwärtig werden Kreuzungen mit dieser Form untersucht.

Für die Ausbildung von Blütenfarbe in der Form von feinen Strichelchen längs den Nerven — hauptsächlich der Flügel — haben MIYAKE, IMAI and TABUCHI (1930) konstatiert, dass diese Eigenschaft gegenüber der ganzfarbigen Blüte einfach rezessiv erscheint. Das hierfür verantwortliche Genpaar will ich mit dem Symbol *Lin—lin* bezeichnen, abgeleitet von *lineatus* = gestrichelt, der rezessiven Eigenschaft entsprechend.

Schliesslich ist noch das in vorliegender Arbeit untersuchte Genpaar *Aeq—aeq* zu erwähnen, dessen dominante Form sowohl bei Bischofsvioletten, Laeliafarbigen wie auch Weissen Blüten (mit *P* und *T*) eine Farbenverstärkung bzw. -ausbildung (bei Weissen Blüten) am oberen Rande der Fahne verursacht, die ich als Terminalverstärkung bezeichnet habe.

SUMMARY.

1. In the chapter on the history the writer gives a more detailed survey and analysis of the results published hitherto on the inheritance of flower colour; then follows a description of the flower colours exam-

ined in the present paper, based on RIDGWAY's Color Standards and Nomenclature and other standard works on the determination of colours. Below is given a synopsis of the most important results obtained.

2. Every formation of flower colour is subject to the fundamental gene for the production of seed coat colour, *P*, and the fundamental gene for whole-coloured seed coat, *T*, being present in a dominant form. All individuals with either *pp* or *tt* (white-seeded and particoloured) have white flowers. The two genes *P* and *T* thus act also in flower colour as fundamental genes.

3. For the formation of different flower colours there is a series of at least three multiple allelomorphs, *V*, v_{lae} and *v*. Together with *P* and *T*, *V* produces bishopsviolet flowers, v_{lae} laelia-coloured flowers while with *v* the flowers remain white. The author knows of another simple flower colour, pale rose-lilac, which is also probably caused by a gene belonging to this series. *V* is dominant over v_{lae} and *v*, v_{lae} over *v*. Coloured flowers are therefore always dominant over white.

4. With respect to *V* and probably also v_{lae} heterozygous plants show a somewhat lighter shade than corresponding homozygous.

5. With the presence of *P* the gene *V* causes definite seed coat colour, subject to the other colour genes for seed coat colour. The formation of flower colour is, however, entirely independent of these colour genes (*C*, *J*, *G*, *B* and possibly *R*). v_{lae} has no effect on the seed coat colour. Thus, there are races of beans with white seeds but laelia-coloured flowers.

6. A description is given of a new type of flower colour, in which the upper margin of the banner petal — especially on the inside — shows a very marked intensification of the colour. This is caused by a dominant gene *Aeq*, which is effective together with both *V* and v_{lae} and *v*. In the latter case the flower is otherwise white while the banner petal exhibitis an upper margin of flesh-colour.

7. In one case the author found that the terminal intensification of the colour on the banner petal, mentioned in par. 6, was caused by two genes. In the cross in question a segregation in the ratio of 9 with terminal intensification : 7 without was obtained.

8. The pair of genes which were found by SHAW (1913) to be the basis of the pair of characters crimson flower colour with purple leaves and stem contra bishopsviolet or waxy pink with waxy brownish yellow coating on the leaves and stem contra laelia-coloured flowers,

are designated by the writer as *Nud—nud*, derived from the recessive character naked = nudus, that is, without purple or waxy coating.

9. The gene-pair, corresponding to the character-pair whole-coloured petals contra streaks (along the nerves with fine, short, coloured streaks), first discovered by MIYAKE, IMAI and TABUCHI, is designated by the writer by the symbol *Lin—lin*, corresponding to the recessive character streaked petals.

10. In addition to their effect on the flower colour the genes *V* and v_{lae} also effect the colour of the stem. *V*-individuals have red stem colour, v_{lae} have rose-coloured stems. In *v*-individuals both rose-coloured and green stems have been met with. MIYAKE, IMAI and TABUCHI have found individuals with green stems which had either red, rose-colour or white flower colour. There are probably here several genes that have not yet been closely examined.

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ERBLICHKEITSVERSUCHE MIT PISUM

IX. FORTGESETZTE STUDIEN ÜBER SEMISTERILE FORMEN

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EINLEITUNG.

DIE hier zu behandelnden Fälle von Semisterilität bei *Pisum* sind die von HÅKANSSON (1932, 1934) und ERNST NILSSON (1933) früher untersuchten und näher beschriebenen. Sie sind von Beginn an mit N.I, N.II, N.III (HÅKANSSON, 1932) und N.IV (HÅKANSSON, 1934) bezeichnet worden, welche Bezeichnungen auch hier beibehalten werden.

Der Semisterilitätsfall N.I wurde in der Form einer einzelnen partiell sterilen Pflanze unter im übrigen fertilen Kreuzungsnachkommen mit unbekannten Eltern entdeckt, der Fall N.II als eine semisterile Pflanze in einer Parzelle der französischen Erbsensorte Sabre mit allen übrigen Pflanzen fertil und Fall N.IV in der Form von semisterilen F_1-Pflanzen in mehreren Kreuzungen zwischen einer Linie der Sorte Extra Rapid und mehreren anderen Erbsensorten. Unter semisterilen Nachkommen nach diesen Originalindividuen hat HÅKANSSON (1932, 1934) eine ringförmige Anordnung von 4 Chromosomen gefunden. Der Fall N.III wurde erst in F_2 einer Kreuzung zwischen den Sorten Automobil und Bohnenerbse entdeckt, die ein Spaltungsverhältnis zwischen fertilen und partiell sterilen Pflanzen von annähernd 1:1 zeigte. In diesem Fall hat sich herausgestellt, dass die zytologischen Verhältnisse von denen der übrigen Fälle abweichen (HÅKANSSON, l. c.).

Durch Untersuchung von Kreuzungen zwischen semisterilen Pflanzen der verschiedenen Serien und zwischen solchen und der hier verwendeten Linie von Extra Rapid, die den x-normalen Typus in der Serie N.IV bildet, ist es HÅKANSSON (1934) festzustellen gelungen, dass in verschiedenen Fällen verschiedene Chromosomen verändert sind. Nur zwei Fälle, N.II und N.III, hatten die gleichen zwei Chromosomenpaare verändert, aber in zytologischer Hinsicht sind sie trotzdem nicht identisch (HÅKANSSON, 1932, 1934). Mit einer willkürlichen Nummerierung der betreffenden Chromosomen von I—IV, hat sich demnach ge-

zeigt, dass folgende Chromosomen von der normalen Konstitution in den verschiedenen Fällen abweichen:

Bei	N. I	die Chromosomen	I	und	II
»	N. II	» »	II	»	III
»	N.III	» »	II	»	III
»	N.IV	» »	III	»	IV

Bei N.I, N.II und N.IV können die gefundenen Verhältnisse sowohl in genetischer wie in zytologischer Hinsicht durch die Annahme eines reziproken Austausches von Teilen zwischen den betreffenden Chromosomen erklärt werden, während die zytologische Erklärung von Fall N.III eine andere ist (HÅKANSSON, 1934). In genetischer Hinsicht verhält sich diese Serie, soweit die Untersuchung bisher vorgeschritten ist, wie die übrigen (ERNST NILSSON, 1933). Bezeichnet man die Chromosomen so wie dies in der *Datura*-Literatur üblich ist, d. h. den normalen Typus von *Pisum* mit 1.2, 3.4, 5.6, 7.8, 9.10, 11.12, 13.14, so können die x-normalen Individuen in den Serien N.I, N.II und N.IV folgendermassen bezeichnet werden:

x-normal	N. I:	1.4, 2.3, 5.6, 7.8 etc.
»	N. II:	1.2, 3.6, 4.5, 7.8 etc.
»	N.IV:	1.2, 3.4, 5.8, 6.7 etc.

Dies wurde als eine für den Leser arbeitsbesparende Introduktion angeführt. In bezug auf die zytologischen Einzelheiten und Beweise sei auf die oben zitierten Arbeiten von HÅKANSSON verwiesen.

Das Ziel der von mir auszuführenden, weiteren rein genetischen Untersuchungen dieser Sterilitätsfälle, das ich vor allem anstrebe, ist eine Feststellung welche Koppelungsgruppen und einzelne Gene bei *Pisum* einen Zusammenhang mit der Semisterilität in den verschiedenen Serien zeigen. Wenn ein gewisser Sterilitätsfall einen Zusammenhang mit gewissen Koppelungsgruppen bzw. Genen zeigt, sind die zwei veränderten Chromosomen in einer bestimmten Weise charakterisiert, was auch für die betreffenden Koppelungsgruppen gilt. Eine auf Grund einer solchen Kenntnis fortgesetzte Inventierung der bekannten Gene dürfte zur Lösung der Frage nach der wirklichen Verteilung der *Pisum*-Gene auf Koppelungsgruppen beitragen können. Der Genanalyse allein ist es bekanntlich noch nicht gelungen eine sichere Übereinstimmung zwischen der Anzahl Koppelungsgruppen und der Anzahl Chromosomen nachzuweisen.

Wenn die Kenntnis vom Zusammenhang zwischen Semisterilität

und verschiedenen Koppelungsgruppen bei *Pisum* grösser geworden ist, wird man auch Aussicht haben einen *gegenseitigen* Austausch von Genen zwischen zwei sicheren Koppelungsgruppen festzustellen, d. h. die *genetische* Äusserung der auf Grund von *zytologischen* Beobachtungen als sehr wahrscheinlich nachgewiesenen reziproken Translokation zwischen nicht homologen Chromosomen.

Bis auf weiteres sind nur zwei Fälle von Zusammenhang zwischen Semisterilität und früher bekannten Anlagen in der *Pisum*-Literatur bekannt, nämlich HAMMARLUNDS Fall von Chromosomenkoppelung zwischen *A* und *Gp* (siehe u. a. HAMMARLUND und HÅKANSSON, 1930) und ferner der Zusammenhang zwischen *R* und der Chromosomenveränderung bei Thibet 7 (PELLEW, 1931). Im ersten Fall handelt es sich leider um zwei Gene, die im Koppelungsschema bisher einsam stehen. *A* hat, soweit mir bekannt, keine sicher konstatierte Koppelung mit einem anderen Gen gezeigt. WELLENSIEK (1928) hat dagegen die Resultate von zwei Kreuzungen veröffentlicht, die auf eine Koppelung zwischen *Gp* und *F* mit einem Crossing-over von ca. 25 % deuten, während andere dihybride Spaltungen, an denen diese beiden Gene teilnehmen, zweifellos freie Kombination zwischen diesen aufweisen (WELLENSIEK, 1927, 1930). Die Koppelung *Gp—F* muss daher bis auf weiteres als allzu unsicher erachtet werden um in diesem Zusammenhang verwendet werden zu können.

In einer vor ein paar Jahren erschienenen Zusammenfassung neuerer Fortschritte in der Genetik (SANSOME and PHILP, 1932) werden in der Übersicht über die Koppelungsgruppen bei *Pisum* (l. c. S. 106) *Gp* und *I* laut Untersuchungen von SVERDRUP (1927) als gekoppelt angegeben. Dies beruht indessen auf einer Verwechslung zwischen den Genen *Gp* und *O*, die nichts miteinander zu tun haben, und einen distinkt verschiedenen phänotypischen Effekt haben, wenn auch beide in rezessiver Form gelbe Hülsen bedingen. Die von SVERDRUP veröffentlichte Koppelung zwischen grüne—gelbe Hülse und gelbe—grüne Kotyledonen bezieht sich auf die Gene *O—I* und nicht *Gp—I* (ERNST NILSSON, 1929, S. 228 und 261—262). Es muss also *Gp* ebenso wie *A* als freistehend aufgefasst werden, weshalb HAMMARLUNDS Semisterilitätsfall unglücklicherweise noch nicht zum Nachweis von gegenseitiger Translokation von Genen verwendet werden kann.

Als Kreuzungsmaterial kann man zu Untersuchungen obengenannter Art ausser in bezug auf die Chromosomenkonstruktion normale Linien mit verschiedenen Genen natürlich auch partiell sterile Pflanzen in den verschiedenen Sterilitätsserien verwenden. Bedeutend weniger

Arbeit erheischend und sicherer ist es natürlich in bezug auf die Chromosomenveränderung homozygote Linien, d. h. x-normale Linien aus den verschiedenen Sterilitätsserien, zu verwenden. Eine Unterscheidung der x-normalen Typen — die abweichenden Primärtypen — in den verschiedenen Fällen bildet daher eine wichtige Vorarbeit für das Studium des Zusammenhanges zwischen Semisterilität und verschiedenen bekannten Genen. Ein Verfügen über die Primärtypen ist auch eine wichtige Voraussetzung für ein genaueres Studium der Gametenbildung bei semisterilen (spaltenden) Individuen.

KREUZUNGEN ZWISCHEN DEN URSPRUNGSRASSEN.

Die *Pisum*-Rassen, die zur Entstehung der verschiedenen hier behandelten Fälle von Semisterilität geführt haben sind für N.I unbekannt, für N.II L.38 Sabre, für N.III L.78 Automobil und L.77 Bohnenerbse, für N.IV, L.34 Extra Rapid und für die in dieser Serie hinsichtlich Spaltung untersuchten Fälle (ERNST NILSSON, 1933) L.8 Witham Wonder, L.11 Lincoln und L.116 American Wonder sowie für den nicht näher untersuchten Fall N.V (diese Bezeichnung wird hier zum erstenmal verwendet) L.89 *wlo*-Linie aus English Wonder (ERNST NILSSON, 1933) und L.93 De Grace.

Von diesen Linien verfüge ich nicht mehr über L.116. Die übrigen Linien sind in den Jahren 1932 und 1933 untereinander gekreuzt worden und ihre F_1-Generationen sind untersucht worden um zu konstatieren, ob sie verschiedene Primärtypen repräsentieren, oder ob die gefundenen Semisterilitätsfälle ihren Ursprung in einzelnen veränderten Pflanzen oder Gameten in den Linien oder Sorten haben. Ausserdem hat L.54 Acacia an dieser Kreuzungsserie teilgenommen, da sie bei Kreuzung mit gewissen anderen Linien Samenabort gegeben hat, der indessen, wie sich später herausstellte, nichts mit Semisterilität zu tun hatte.

Folgende Kreuzungen wurden untersucht:

Kreuzung	I.	L.38 Sabre	× L.78	Automobil
»	II.	»	× L.34	Extra Rapid
»	III.	»	× L.89	*wlo* aus English Wonder
»	IV.	»	× L.54	Acacia
»	V.	L.78 Automobil	× L.34	Extra Rapid
»	VI.	»	× L. 8	Witham Wonder

Kreuzung	VII.	L.78 Automobil	× L.11 Lincoln
»	VIII.	»	× L.89 *wlo*
»	IX.	»	× L.93 De Grace
»	X.	»	× L.54 Acacia
»	XI.	L.77 Bohnenerbse	× L.38 Sabre
»	XII.	»	× L.78 Automobil
»	XIII.	»	× L.34 Extra Rapid
»	XIV.	»	× L. 8 Witham Wonder
»	XV.	»	× L.11 Lincoln
»	XVI.	»	× L.89 *wlo*
»	XVII.	»	× L.93 De Grace
»	XVIII.	»	× L.54 Acacia
»	XIX.	L.34 Extra Rapid	× L. 8 Witham Wonder
»	XX.	L. 8 Witham Wonder	× L.38 Sabre
»	XXI.	»	× L.89 *wlo*
»	XXII.	»	× L.93 De Grace
»	XXIII.	L.11 Lincoln	× L.38 Sabre
»	XXIV.	»	× L.34 Extra Rapid
»	XXV.	»	× L. 8 Witham Wonder
»	XXVI.	»	× L.89 *wlo*
»	XXVII.	»	× L.54 Acacia
»	XXVIII.	L.89 *wlo*	× L.34 Extra Rapid
»	XXIX.	»	× L.93 De Grace
»	XXX.	»	× L.54 Acacia
»	XXXI.	L.93 De Grace	× L.38 Sabre
»	XXXII.	»	× L.34 Extra Rapid
»	XXXIII.	L.54 Acacia	× L.34 Extra Rapid
»	XXXIV.	»	× L. 8 Witham Wonder
»	XXXV.	»	× L.93 De Grace

Mit Ausnahme von L.11 Lincoln × L.93 De Grace sind also alle möglichen Kombinationen untersucht; aber das Fehlen dieser Kreuzung bedeutet nichts für die Vollständigkeit der Resultate, da alle übrigen Kreuzungen mit L.93 und L.11 ausgeführt sind. Das Ergebnis der Pollenuntersuchung von F_1 ist in Schema 1 schematisch dargestellt; F bedeutet dort, dass alle oder so gut wie alle Pollenkörner normal entwickelt sind, und St, dass etwa die Hälfte der Pollenkörner taub sind.

Aus den Resultaten geht hervor, dass L.34 Extra Rapid bei Kreuzung mit sämtlichen übrigen Linien in F_1 Semisterilität ergeben hat, wodurch bewiesen ist, dass L.34 einen anderen Primärtypus als diese

	L.38							
L.78	F	L.78						
L.77	F	F	L.77					
L.34	St	St	St	L.34				
L.8	F	F	F	St	L.8			
L.11	F	F	F	St	F	L.11		
L.89	F	F	F	St	F	F	L.89	
L.93	F	F	F	St	F	X	F	L.93
L.54	F	F	F	St	F	F	F	F

Schema 1. Schema über Kreuzungen zwischen den Ursprungsrassen zu den verschiedenen Semisterilitätsfällen. F = fertile F_1. St = semisterile F_1.

und daher den x-normalen Typus in N.IV darstellt. Von den hier erwähnten F_1-Generationen hat HÅKANSSON Kreuzg. XIX, XXIV, XXVIII und XXXIII untersucht und stets Amphibivalente gefunden (HÅKANSSON, 1934). Ausserdem hat der genannte Forscher F_1 nach L.34 × L.49 Luxuria und L.34 × L.76 Frühe niedrige untersucht und auch hier Ringe gefunden (l. c.); gleichzeitig ist von mir in diesen Fällen Pollenabort konstatiert worden. Indessen dürfte nicht nur meine L.34 aus Extra Rapid einen abweichenden Primärtypus darstellen sondern mit grösster Wahrscheinlichkeit die Sorte in ihrer Gänze, die selbst eine aus der Sorte Rapid ausgelesene Linie darstellt (HAMMARLUND, 1927) da die Kreuzung Solo × Extra Rapid in HAMMARLUNDs Material auch zu einer semisterilen F_1 geführt hat (HÅKANSSON, 1931), und meine L.34 von HAMMARLUND nicht verwendet worden ist. Die Sorte bildet im unvermengten Zustande offenbar eine reine Linie mit abweichender Chromosomenkonstitution, nämlich 1.2, 3.4, 5.8, 6.7 u. s. w. (HÅKANSSON, 1934). Dass Extra Rapid einem abweichenden Primärtypus angehört ist i. ü. schon von HÅKANSSON (1934) hervorgehoben worden. In noch ein paar nicht veröffentlichten und in dieser Arbeit nicht näher berührten Fällen

habe ich Semisterilität in Extra Rapid-Kreuzungen gefunden, nämlich in F_1 nach L.34 × L.32 Stensärt und L.34 × L.43 Emerald gem.

Alle anderen Linien, die als Eltern zu den in Schema 1 zusammengestellten Kombinationen verwendet worden sind, haben dagegen identische Chromosomenkonstitution, da sie bei Kreuzung untereinander stets eine fertile F_1 geben. Sämtliche diese Linien haben ausserdem in einer sehr grossen Anzahl von Kreuzungen mit anderen *Pisum*-Linien und -Sorten teilgenommen, die sowohl in praktischer wie theoretischer Absicht ausgeführt worden sind, und hierbei stets fertile Nachkommen gegeben, weshalb sie dem normalen Primärtypus mit der Konstitution 1.2, 3.4, 5.6, 7.8, 9.10, 11.12, 13.14 angehören müssen.

Damit ist auch erwiesen, dass eine *einzelne* Pflanze mit einer abweichenden Chromosomenkonstitution einer der Elternsorten den Sterilitätsfall N.III (Bohnenerbse × Automobil) verursacht haben muss. Die Serie N.II stammt von einer einzelnen Pflanze der Sorte Sabre (damals nicht als reine Linie gezogen), eine Pflanze die entweder ihrerseits von einer anderen, schon früher semisterilen Pflanze der gleichen Sorte herstammt oder direkt aus der Vereinigung zwischen einer normalen und einer veränderten Gamete entstanden ist. Dasselbe gilt offenbar für den Sterilitätsfall N.V aus Kreuzung L.89 *wlo* × L.93 De Grace, was schon in einer früheren Arbeit betont worden ist (ERNST NILSSON, 1933 a). Der Fall N.I hat sich vom Beginn an als spontan erwiesen.

Durch die in diesem Kapitel erwähnten Kreuzungen haben also zwei Primärtypen unterschieden werden können, nämlich der normale Primärtypus, zu dem unter den hier verwendeten Linien L.38, L.78, L.77, L.8, L.11, L.89, L.93 und L.54 gehören, sowie ein abweichender Primärtypus, zu dem L.34 gehört, und der den x-normalen Typus in N.IV-Spaltungen bildet.

DIE PRIMÄRTYPEN IN DER SERIE N. III.

Aus D_1-Nachkommen nach semisterilen Pflanzen in der Serie N.III sind im Laufe der Jahre mehrere fertile Linien zu Kreuzungen untereinander ausgelesen worden, um eine Klassifikation der Linien in o-normale und x-normale und eine Untersuchung des Zahlenverhältnisses zwischen diesen beiden Typen zu ermöglichen.

Im Jahre 1932 wurde L.77 Bohnenerbse, deren Charakter als normaler Primärtypus damals unbekannt war, mit 4 fertilen Linien aus der N.III-Serie gekreuzt, die später als N.III, L.22, N.III, L.23,

N.III, L.24 und N.III, L.30 bezeichnet worden sind (diese Linien gehören nicht zu meiner gewöhnlichen Liniensammlung, weshalb diese abweichenden Bezeichnungen verwendet wurden). Die Kreuzungen ergaben folgende Resultate:

L.77 × N.III, L.23: fertile F_1
» × N.III, L.24: » »
» × N.III, L.30: » »
» × N.III, L.22: semisterile F_1

Gleichwie L.77 gehören demnach N.III, L.23, N.III, L.24 und N.III, L.30 zum normalen Primärtypus, während *N.III, L.22 einem abweichenden Primärtypus angehört*, bei dem laut HÅKANSSON (1934) die Chromosomen II und III verändert sind. Letztere Linie bildet m. a. W. den x-normalen Typus in N.III.

Unmittelbar nach dieser Entdeckung wurde 1933 und dann auch 1934 eine Serie neuer Kreuzungen zwischen N.III, L.23, die als Indikatorlinie und als Vater fungierte, und 26 neuen fertilen Linien aus N.III ausgeführt. Hierbei wurden folgende Resultate erhalten:

N.III, L. 1 × N.III, L.23: fertile F_1
N.III, L. 2 × » : » »
N.III, L. 3 × » : » »
N.III, L. 4 × » : » »
N.III, L. 5 × » : » »
N.III, L. 6 × » : » »
N.III, L. 7 × » : » »
N.III, L. 8 × » : sterile »
N.III, L. 9 × » : fertile »
N.III, L.10 × » : » »
N.III, L.11 × » : » »
N.III, L.12 × » : » »
N.III, L.13 × » : sterile »
N.III, L.14 × » : » »
N.III, L.15 × » : » »
N.III, L.16 × » : » »
N.III, L.17 × » : fertile »
N.III, L.18 × » : » »
N.III, L.19 × » : sterile »
N.III, L.20 × » : fertile »
N.III, L.21 × » : » »

N.III, L.25 × N.III, L.23: fertile F_1
N.III, L.26 × » : sterile »
N.III, L.28 × » : fertile »
N.III, L.29 × » : » »
N.III, L.43 × » : sterile »

Hier sind also die Linien N.III, L.8, N.III, L.13—N.III, L.16, N.III, L.19, N.III, L.26 sowie N.III, L.43 x-normal, während die übrigen 15 Linien o-normal sind. Von sämtlichen 30 in den Jahren 1933—1935 untersuchten Linien sind im ganzen 21 o-normal und 9 x-normal. Das gefundene Verhältnis weicht also ziemlich beträchtlich von dem erwarteten Verhältnis 1 : 1 ab.

Gefundenes Verhältnis $1{,}_{40} : 0{,}_{60}$
$m_K = 0{,}_{182}$ Diff./$m_K = 2{,}_2$

Die Abweichung vom Idealverhältnis ist nicht signifikativ, aber die Anzahl untersuchter Linien ist auch nicht gross. Es sind daher neue fertile Linien zwecks späterer Klassifikation ausgelesen worden.

Es soll vielleicht erwähnt werden, dass auch das Verhältnis fertile : sterile unter den Nachkommen nach semisterilen Individuen in der Serie N.III recht stark von 1 : 1 abgewichen ist (ERNST NILSSON, 1933 a).

1934 wurde zur Kontrolle der Gametenverteilung auf normale und solche mit reziproker Translokation eine Serie von Kreuzungen zwischen semisteriler F_1 und o-normalen bzw. x-normalen N.III-Linien sowie reziprok ausgeführt. Diese Kreuzungen gaben in F_1 folgende Resultate:

Semisterile F_1 × o-normal =	33	fertile :	40	sterile
» » × x-normal =	26	» :	30	»
o-normal × semisterile F_1 =	23	» :	28	»
x-normal × » » =	30	» :	29	»
Zusammen:	112	fertile :	127	sterile

Das gefundene Verhältnis ist hier $0{,}_{94}$ fertile : $1{,}_{06}$ sterile pro 2; $m_K = 0{,}_{064}$ und Diff./$m_K = 0{,}_{98}$. Diese Zahlen berechtigen also nicht zur Annahme, dass die Gametenbildung den einen oder den anderen Genotypus begünstigt, und zwar weder beim männlichen noch beim weiblichen Geschlecht.

Ausser den genannten Kreuzungen wurden 1933 auch einige Kontrollkreuzungen ausgeführt, um die nach 1932-Kreuzungen schon 1933

ausgelesene x-normale Linie N.III, L.22 und die als Indikator gedachte o-normale N.III, L.23 zu kontrollieren. Ausserdem wurde die Kreuzung L.77 × N.III, L.22 in reziproker Form zwecks weiterer Kontrolle wiederholt. Diese Kreuzungen gaben folgende Resultate:

N.III, L.22 × N.III, L.23: sterile F_1
» × L.11, Lincoln: sterile F_1
N.III, L.23 × » : fertile F_1
N.III, L.22 × L.77 Bohnenerbse: sterile F_1

Die Kontrollkreuzungen gaben gerade die erwarteten Resultate, wodurch sicher bewiesen ist, dass es gelungen ist aus der Serie N.III die o-normalen und die x-normalen Typen auszuscheiden, ein Resultat, das als Grund für weitere Untersuchungen grössere Bedeutung hat, als seine Unbedeutenheit an und für sich anzeigt.

DIE PRIMÄRTYPEN DER SERIE N. I.

Erst im Jahre 1933 standen fertile Linien aus N.I, und zwar 6, zu Kreuzungen zur Verfügung. Diese wurden gegenseitig gekreuzt, aber die Blühte war sehr schlecht, weshalb nicht alle Kombinationen realisiert werden konnten. F_1 folgender Kreuzungen konnten indessen 1934 untersucht werden:

N.I, L.1 × N.I, L.2: fertile F_1
» × N.I, L.3: » »
» × N.I, L.6: » »
N.I, L.3 × N.I, L.2: » »
N.I, L.4 × N.I, L.1: » »
» × N.I, L.2: » »
» × N.I, L.6: » »
N.I, L.5 × N.I, L.2: » »
» × N.I, L.3: » »
» × N.I, L.6: » »

N.I, L.1 ist also identisch mit N.I, L.2, N.I, L.3, N.I, L.4 und N.I, L.6. N.I, L.2 ist ausserdem identisch mit N.I, L.3, N.I, L.4 und N.I, L.5, N.I, L.4 identisch mit N.I, L.6 sowie N.I,L.5 identisch mit N.I, L.6, woraus folgt, dass sämtliche 6 Linien von 1934 identisch sind.

Eine dieser fertilen Linien, N.I, L.2, wurde 1933 mit L.11 Lincoln gekreuzt, deren Zugehörigkeit zum normalen Typus durch mehrere Kreuzungen festgestellt worden ist. Drei Kreuzungen N.I, L.2 × L.11

Lincoln haben semisterile F_1 gegeben. N.I, L.2 und damit auch die übrigen oben erwähnten fertilen Linien sind demnach x-normal.

Im Jahre 1934 wurde eine weitere Anzahl von fertilen Linien zu Kreuzungen verwendet. Die Untersuchung von F_1 ergab folgendes Resultat:

N.I, L. 9 ×	N.I, L. 1:	fertile F_1
N.I, L.11 ×	» :	sterile »
N.I, L.12 ×	» :	» »
N.I, L. 2 ×	N.I, L.11:	» »
N.I, L. 3 ×	» :	» »
N.I, L.12 ×	N.I, L. 6:	» »
N.I, L.12 ×	N.I, L. 7:	» »
N.I, L.11 ×	N.I, L. 9:	» »
» ×	N.I, L.13:	fertile »
N.I, L.13 ×	N.I, L.12:	» »

Die zu diesen Kreuzungen benützten Linien N.I, L.1, N.I, L.2, N.I, L.3 und N.I, L.6 sind, wie bereits erwähnt, x-normal, woraus folgt, dass die neuen Linien N.I, L.7 und N.I, L.9 x-normal, wogegen N.I, L.11, N.I, L.12 und N.I, L.13 o-normal sind.

Die F_1-Untersuchung der beiden Jahre hat also gezeigt, dass von 12 Fertillinien in N.I 3 o-normal und 9 x-normal sind. Das Verhältnis ist:

$0{,}_5$ o-normale : $1{,}_5$ x-normale

$m_K = 0{,}_{289}$; Diff./$m_K = 1{,}_{73}$

Trotz der grossen Abweichung vom idealen Verhältnis 1 : 1 kann das gefundene Verhältnis also nicht mit Sicherheit als vom idealen verschieden aufgefasst werden. In diesem Fall muss indessen eine grössere Anzahl fertiler Linien untersucht werden, da es sehr wahrscheinlich ist, dass das Verhältnis zwischen o-normalen und x-normalen Linien hier wirklich ein anderes als das ideale ist, wenn auch die geringe Anzahl bisher untersuchter Linien eine Feststellung dieses Unterschiedes nicht gestattet hat.

Wie schon in einer früheren Publikation (ERNST NILSSON, 1933 a) hervorgehoben worden ist, spaltet N.I in einem Verhältnis, das sich mehr dem Verhältnis $0{,}_5$ fertile : 1 sterile nähert als 1 fertile : 1 sterile, was auch der Fall sein würde, wenn der eine fertile Typus letal wäre. Die letzten Untersuchungen haben indessen gezeigt, dass keiner der fertilen Typen letal ist; aber gleichzeitig stehen sie nicht im Widerspruch zur Annahme, dass der eine Typus weniger vital als der andere

ist. Dies würde solchenfalls für den o-normalen Typus gelten. Umfangreichere Untersuchungen sind notwendig, bevor dieser Fall klargelegt sein wird, und bevor eine eingehendere Diskussion motiviert erscheint.

Zur Kontrolle der N.I-Linien wurden 1934 auch einige Kreuzungen mit anderen Linien ausgeführt, deren Konstitution bekannt war. Es waren dies folgende:

N.I, L.13 × L.34 Extra Rapid: nicht mehr als $^1/_2$-sterile F_1

L.77 Bohnenerbse × N.I, L.12: fertile F_1.

N.III, L.22 (x-normal) × N.I, L.13: nicht mehr als $^1/_2$-sterile F_1

Das Ergebnis dieser Kreuzungen stimmt vollkommen mit dem früherer Untersuchungen überein.

Auch im Fall N.I ist es demnach gelungen die zwei Primärtypen zu unterscheiden, die o-normale und die x-normale 1.2, 3.6, 4.5, 7.8 etc.

DIE PRIMÄRTYPEN DER SERIE N. II.

Folgende Kreuzungen wurden 1934 ausgeführt und 1935 untersucht:

N.II, L. 1 × N.II, L.4: sterile F_1
N.II, L. 2 × » : » »
N.II, L. 4 × N.II, L.3: » »
N.II, L.11 × N.II, L.4: » »

Die Linie N.II, L.4 weicht also von den übrigen untersuchten Linien ab, weshalb auch hier die zwei Primärtypen separiert sind. Dagegen ist noch nicht festgestellt, welche von den untersuchten Linien o-normal bzw. x-normal sind.

BISHER FESTGESTELLTE PRIMÄRTYPEN BEI PISUM.

Ausser dem Normaltypus, zu dem u. a. mehrere Linien meines Materials laut Experiment gehören, sind bisher, soweit mir bekannt, in der *Pisum*-Literatur drei Primärtypen erwähnt, nämlich HAMMARLUNDS K-Linie (HAMMARLUND, 1928), Thibetan pea 7 (PELLEW and SANSOME, 1931) und Extra Rapid (HÅKANSSON, 1931, 1934). In dieser Arbeit sind ausserdem noch zwei Primärtypen, x-normal in N.III und x-normal in N.I, identifiziert sowie die beiden Primärtypen in N.II unterschieden aber noch nicht identifiziert worden. Die sicher festgestellten Primärtypen bei *Pisum* sind demnach:

Primärtypus A = der normale Typus (1.2, 3.4, 5.6, 7.8 etc.)
» B = HAMMARLUNDS K-Linie
» C = Thibetan pea 7
» D = Extra Rapid (1.2, 3.4, 5.8, 6.7 etc.)
» E = x-normal aus N.III (mit verändertem Chromosom II und III)
» F = x-normal aus N.I (1.4, 2.3, 5.6, 7.8 etc.)
» G = x-normal aus N.II (1.2, 3.6, 4.5, 7.8 etc.)

Englische Untersuchungen (l. c.) haben festgestellt, dass die Primärtypen B und C ein gemeinsames und ein spezielles Chromosom verändert haben; es verbleibt nun zu untersuchen, ob eines von diesen drei Chromosomen mit einem der von HÅKANSSON identifizierten identisch ist, und ob die Primärtypen B und C einem der Primärtypen D—G gleich sind.

Bei Kreuzungen zwischen in verschiedener Weise veränderten Linien hat man ausser in verschiedenem Grad sterile Pflanzen die beiden mit den Eltern übereinstimmenden Primärtypen wieder zu erwarten. In Kreuzungen zwischen x-normalen N.I und N.IV (1.4, 2.3, 5.6, 7.8 etc. × 1.2, 3.4, 5.8, 6.7 etc.), die zwei Ringe mit je vier Chromosomen geben (HÅKANSSON, 1934), hat man indessen vier verschiedene Primärtypen zu erwarten: 1) den Normaltypus, 2) einen mit x-normal aus N.I übereinstimmenden Typus, 3) einen mit x-normal aus N.IV (Extra Rapid) übereinstimmenden und 4) einen neuen Primärtypus 1.4, 2.3, 5.8, 6.7 etc., d. h. homozygot in bezug auf die Veränderung bei 4 Chromosomen, aber doch mit allen Chromosomenteilen disomisch anwesend. Dieser neue Typus ist jedoch experimentell noch nicht nachgewiesen, Versuche hierzu sind aber im Gange.

EIN ABWEICHENDER TYPUS IN N. IV-SPALTUNGEN.

In sämtlichen spaltenden N.IV-Parzellen sowie in Kreuzungen zwischen N.IV und anderen Serien wurde 1934 ein regelmässiges Auftreten eines stark abweichenden Phänotypus beobachtet. Die betreffenden Pflanzen waren niedriger und viel zarter als normale Pflanzen sowie heller grün, was wahrscheinlich darauf beruhte, dass sie dünnere Blätter hatten und daher mehr transparent als normale waren. Am charakteristischesten waren jedoch die Stipeln dieser Pflanzen, die schmaler und spitziger waren als gewöhnlich und weniger aber schärfer als normal markierte Zähne an der Basis zeigten (Fig. 1). Dieser Typus hatte

sehr schlechte Vitalität, die durch die anstrengenden Milieuverhältnisse in diesem Jahre sicherlich noch mehr herabgesetzt wurde. Mehrere dieser Pflanzen gingen vor der Samenreife zugrunde, und Samen wurden von keiner erhalten, vielleicht darauf beruhend, dass von Dozent ARTUR HÅKANSSON soviele Blütenknospen wie möglich fixiert worden sind. Im Jahre 1935 wurde jedoch eine unbedeutende Anzahl reifer Samen von diesem Typus erhalten.

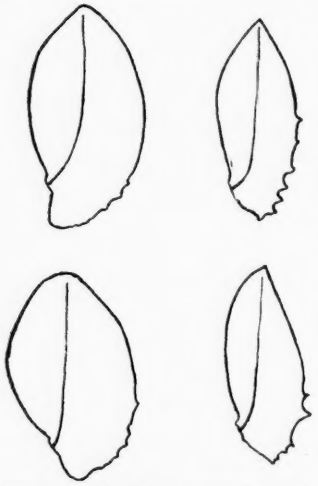


Fig. 1. Links Stipeln von Normalpflanzen und rechts eines in N.IV-Spaltungen aufgetretenen, abweichenden Typus.

Dieser Typus erinnert in seinen äusseren (nicht physiologischen) Eigenschaften nicht wenig an *Pisum elatius*, wie es von SCHEIBE (1934) beschrieben wird.

In einigen F_2-Parzellen nach Extra Rapid $\times$ Normallinien wurde die Anzahl abweichender und normaler Pflanzen bestimmt, wobei resultierte:

20 abweichende : 189 normale.

Bevor sich eine Diskussion dieses Verhältnisses lohnt, müssen die Zahlen aber erst stark erhöht werden. Da der in Rede stehende Typus für N.IV-Spaltungen charakteristisch ist und in den übrigen Serien nicht vorkommt, ist es am wahrscheinlichsten, dass er gerade mit den für N.IV kennzeichnenden Chromosomenstörungen einen Zusammenhang hat. Die zytologischen Verhältnisse, die diesen Typus kennzeichnen, werden in diesem Heft von HÅKANSSON besprochen (HÅKANSSON, 1936).

INTERSTERILITÄT ALS ARTGRENZE.

Auf Grund sowohl früher wie hier vorgelegten Materials ist es klar, dass *Pisum* in verschiedene intrafertile und intersterile Gruppen von ganz anderer Natur als die Gruppen eingeteilt werden kann, deren Existenz auf Selbststerilitätsgene zurückzuführen ist. Hier beruht die Sterilität anstatt dessen darauf, dass Gameten mit einem gewissen Genotypus funktionsuntauglich sind. Gewisse Genkombinationen sind also in der Haplophase letal, und die Sterilität ist also klar haplontisch (MÜNTZING, 1930).

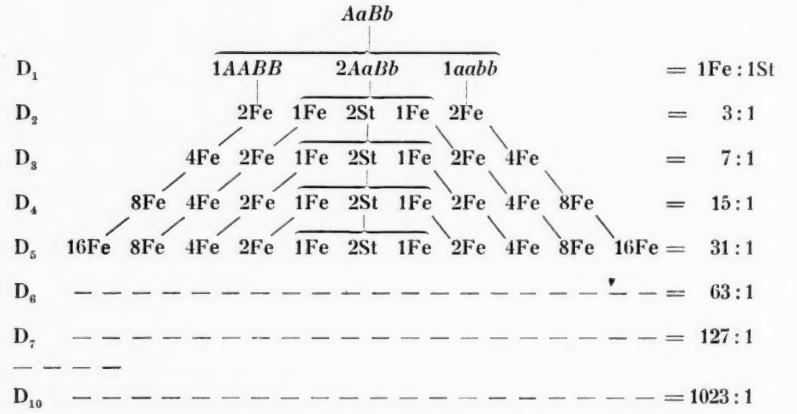
Intersterilität dieser Art — Sterilität von Kreuzungsprodukten — ist eine häufig vorkommende Erscheinung bei Kreuzung zwischen kreuzungsfähigen Arten, und auch dann ist es wahrscheinlich, dass die Sterilität selektiv ist. Auch wenn eine solche Sterilität also für Kreuzungen zwischen relativ nahestehenden Arten (Ökospezies) kennzeichnend ist, bildet indessen das Vorkommen solcher Gametenletalität an und für sich keine Artgrenze, was sowohl Untersuchungen von *Datura*, *Zea*, *Galeopsis* und *Pisum* gezeigt haben. Bei *Datura* hat man gefunden (BLAKESLEE, 1934), dass ein gewisses Verbreitungsgebiet durch einen gewissen Primärtypus charakterisiert wird. Man hat also eine gleichzeitige geographische (ökologische oder entstehungshistorische?) und genotypische Differenzierung in Gruppen gefunden. Bei *Pisum* hat sich gezeigt, dass fünf untersuchte Fälle in HÅKANSSONS und meinem Material mit grösster Wahrscheinlichkeit spontan entstanden sind, oder jedenfalls, dass die Chromosomenveränderung, die den Grund für die Semisterilität bildet, nicht für das Material charakteristisch ist, in dem sie entdeckt worden ist. Solchenfalls ist es unmöglich die Intersterilität als einen Beweis für einen Artunterschied aufzufassen. MÜNTZING (l. c.) ist beim Arbeiten mit *Galeopsis* auch zu dem Resultat gekommen, dass der Unterschied zwischen intra- und interspezifischer Sterilität nur ein Gradunterschied ist.

Will man die Intersterilität vorliegender Art als Artgrenze auffassen, so verbleibt, wenn man konsequent sein will, nur die Möglichkeit auch die intersterilen Gruppen von *Pisum* u. a. als Arten (oder wenn man so will Unterarten) aufzufassen. Rein theoretisch ist hiergegen vielleicht nicht viel einzuwenden, da man zuweilen andere Arten aus weniger festen Gründen als selektive Sterilität im Zusammenhang mit Chromosomenstörungen aufgestellt hat. Eine Aufstellung von Primärtypen als Arten würde indessen unserem Sinn für Proportionen in allzu herausfordernder Weise zuwiderlaufen, um — ohne diesen Sinn ausser Funktion zu setzen — einen solchen Schritt wagen zu wollen.

Man kennt Beispiele, dass in der Natur vorkommende Arten, die sich miteinander kreuzen und ziemlich fertile Bastarden bilden können, sich trotzdem gut getrennt halten und die Bildung von Bastardpopulationen mit den Eltern als Extremtypen nicht zulassen. Ein solches Beispiel hat man in den Arten *Geum urbanum* und *Geum rivale* (WINGE, 1926). Die gleiche Erscheinung findet man an sich selbst überlassenen Nachkommen einer sterilen *Pisum*-Pflanze. Wenn wir die einfachste Möglichkeit wählen, eine Zygote nach Vereinigung einer

Gamete mit reziproker Translokation bei zwei Chromosomen und einer Normalgamete, d. h. eine Gamete mit der Konstitution, die die Majorität in der Art charakterisiert, finden wir ja, dass diese nur vitale Gameten gleich jenen der beiden Eltern oder wenigstens nur in seltenen Ausnahmefällen Rekombinationsgameten bildet. Im einfachsten Fall werden diese Gameten in gleicher Anzahl gebildet und funktionieren gleich, und die beiden Primärtypen sind gleich vital (vielleicht ist dies jedoch nicht Regel). Wir erhalten dann den in Schema 2 dargestellten Verlauf.

Was ist hier geschehen? Ja, eine natürliche Selektion der Elterntypen und eine Ausscheidung des Bastardtypus, gerade wie bei der


AaBb
D1 1AABB 2AaBb 1aabb = 1Fe : 1St
D2 2Fe 1Fe 2St 1Fe 2Fe = 3 : 1
D3 4Fe 2Fe 1Fe 2St 1Fe 2Fe 4Fe = 7 : 1
D4 8Fe 4Fe 2Fe 1Fe 2St 1Fe 2Fe 4Fe 8Fe = 15 : 1
D5 16Fe 8Fe 4Fe 2Fe 1Fe 2St 1Fe 2Fe 4Fe 8Fe 16Fe = 31 : 1
D6 = 63 : 1
D7 = 127 : 1
D10 = 1023 : 1

Schema 2. Der sterile Typus wird aus sich selbst überlassenen Nachkommen einer semisterilen Pflanze ziemlich schnell ausgeschieden, und die Primärtypen, die die Eltern bildeten, werden — abgesehen von Crossing-over-Produkten — zu den hauptsächlich vorkommenden Biotypen.

Kreuzung zwischen zwei Ökospezies. Die Ähnlichkeit wird noch grösser, wenn man in Betracht zieht, dass auch jene Gene, die in den betroffenen Chromosomen liegen, zufolge der Catenation bei der Gametenbildung »zusammenhalten», sodass wir — abgesehen von einzelnen Crossing-over-Gameten — auch nach einigen Generationen den morphologischen Typus der Eltern, soweit er von diesen Genen abhängt, »reingezüchtet» durch natürliche Selektion erhalten. Umso mehr Chromosomen voneinander abhängig sind und einander komplettieren, desto grösser ist die Anzahl Gene, die »zusammenhalten», und umso auffallender ist die morphologische Differenzierung (siehe *Oenothera*).

Es soll jedoch hervorgehoben werden, dass eine derartige allmähliche Ausscheidung der Bastardtypen in den Nachkommen nach einem semisterilen Individuum nur für autogame Arten gilt, insofern nicht gleichzeitig Vitalitätsgene tätig sind, oder der Bastard an und für sich weniger vital ist, Möglichkeiten die eine nähere Untersuchung verdienen.

ZUSAMMENFASSUNG.

1. Die Abhandlung behandelt die Ergebnisse der letzten Jahre der rein genetischen Bearbeitung der semisterilen Serien, die Gegenstand der Untersuchung seitens Dozent ARTUR HÅKANSSON und Verf. sind. In der Einleitung werden einige Richtlinien für die folgende genetische Arbeit angegeben.

2. Kreuzungen zwischen den Ursprungssorten der verschiedenen Sterilfälle zeigen, dass alle diese mit Ausnahme von Extra Rapid dem normalen Primärtypus angehören. Extra Rapid bildet einen abweichenden Primärtypus (der x-normale Typus in N.IV). Damit ist auch gezeigt, dass die gefundenen Sterilfälle mit Ausnahme von N.IV spontan entstanden sind.

3. Drei neue abweichende Primärtypen sind aus N.III, N.I und N.II ausgeschieden worden (die x-normalen Typen dieser Serien).

4. Es wird eine Übersicht über bisher veröffentlichte sichere Primärtypen bei *Pisum* mitgeteilt (die Primärtypen A, B, C, D, E, F und G).

5. Ein in den N.IV-Spaltungen regelmässig auftretender, morphologisch abweichender, subletaler Phänotypus wird erwähnt.

6. Es wird hervorgehoben, dass Intersterilität mit selektiver Wirkung, beruhend auf Letalität gewisser Genkombinationen, nicht als artbegrenzender Charakter aufgefasst werden kann. Bei Kreuzung von zwei Primärtypen bei einer autogamen Art wird der Bastardtypus aus den Nachkommen allmählich ausgeschieden. Je komplizierter der Fall, umso grösser der morphologische und physiologische Effekt einer solchen Selektion.

Eslöv im September 1935.

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INHALT.

Einleitung 167
Kreuzungen zwischen den Ursprungsrassen 170
Die Primärtypen der Serie N.III 173
Die Primärtypen der Serie N.I 176
Die Primärtypen der Serie N.II 178
Bisher festgestellte Primärtypen bei *Pisum* 178
Ein abweichender Typus in N.IV-Spaltungen 179
Intersterilität als Artgrenze 180
Zusammenfassung 183
Zitierte Literatur 183

A SEMI-LETHAL CAUSING EXCEPTIONAL SEX-RATIOS IN DROSOPHILA MELANOGASTER

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IN this paper a sex-linked, semi-lethal gene will be described which seems to be very similar in kind to the one described earlier by MORGAN (1929). As our case has proved easy to analyse, we have thought it worth while giving a brief description of it.

I. THE OCCURRENCE OF THE SEMI-LETHAL *ls* AND THE SEX-RATIOS PRODUCED.

In an experiment containing triploids with two wild-type-bearing attached X-chromosomes and one free X-chromosome, bearing the mutant genes *y*, *cv*, *ct*, *v*, *g*, *f*, we intended to use all equational daughters showing any of the mutant characters in out-crossing for further analysis. When NORDENSKIÖLD, on Oct. 31, 1932, made a count, she found a *yellow* daughter, which was crossed to a *Bar* male (culture 6730, Table 1). The result was 18 *y* females, 2 *B* super-females and 86 *B* males. *Yellow* females from this culture were again crossed to *B* males, and this was repeated for several generations, using pair-cultures as well as those with several females, five at most (Table 1). In all these cultures it was evident that the *yellow* females had attached X-chromosomes and that there was an excess of males in the progeny, although this excess was rather fluctuating. In total there were 1097 diploid females and 6885 males, which is equivalent to 86,3 % males among the diploids. If, as may *a priori* be assumed, the excess of males is due to some kind of semi-lethality among the females, this lethality may be estimated to be

$$100(6885 - 1097)/6885 = 84{,}1\ \%.$$

It should also be observed that there occurred 2 heterozygous *Bar* females, through detachment of the attached X:s, but that no *yellow* males were found. The assumed semi-lethal gene has been denoted *ls*.

TABLE 1. *Offspring of females homozygous with respect to y ls and with attached X:s when mated to Bar males.*

Culture number	♀♀			♂♂		Culture number	♀♀			♂♂	
	y	*B*	*B* sup. fem.	*B*	*y*		*y*	*B*	*B* sup. fem.	*B*	*y*
6730	18		2	86		6779	10			75	
6735	7			123		6780	9			90	
6736	15			97		6781	7			100	
6737	5			75		6782	27		3	93	
6738	8			88		6783	29			131	
6739	13			73		6784	13			68	
6740	3			89		6785	18			42	
6741	4			80		6786	26			130	
6742	4			99		6787	15			93	
6743	0			43		6788	24		1	87	
6744	7			94		6789	18			77	
6746	24			115		6790	2			30	
6747	4			75		6791	18	1	1	72	
6748	5			88		6792	8			49	
6749	4			50		6794	17			96	
6750	11			88		6795	17			92	
6751	19			99		6796	7			43	
6752	19			93		6797	15			113	
6753	0			28		6798	9			69	
6754	3			68		6799	18			93	
6755	0			10		8100	26			101	
6756	8			90		8101	6			89	
6757	33		5	78		8102	8			74	
6758	18			91		8103	9			70	
6759	12			80		8104	8			80	
6760	33			97		8108	18			79	
6761	25		1	129		8109	12			79	
6762	31			140		8111	17			71	
6763	20			91		8112	19			95	
6764	21			92		8113	8			83	
6765	9	1	2	83		8114	8			77	
6766	5			98		8115	11			84	
6767	17		3	126		8116	5			72	
6768	25			95		8117	3			61	
6769	38		1	142		8118	0			10	
6770	16			87		8119	2			14	
6771	6			71		8120	7		1	80	
6772	14			84		8121	16			73	
6773	4			39		8122	10			36	
6774	7			82		8123	4			82	
6775	49			121		8124	10			78	
6776	6			86							
6777	6			45		Total	1095	2	20	6885	0
6778	5			46							

Later on the low-female-producing *yy* females were maintained in mass-cultures, containing *yy* females and *Bar* males. From time

to time the cultures were examined and now and then heterozygous *B* females were found, whereas up to date no *yellow* male has been found in these cultures. Altogether 5 females containing *B* in one X and *y* as well as *ls* in the other have been out-crossed. The results

TABLE 2. *Offspring of 5 females with Bar in one X-chromosome and y ls in the other when mated to different males.*

Culture number	Total females	♂ ♂				Total males
		B	*y*	+	*yB*	
8126	135	21	1	26	1	49
8130	176	58	9	50	21	138
8137	141	53	4	20	8	85
8141	173	47	8	36	16	107
8146	193	48	12	32	3	95
Total	818	227	34	164	49	474

are shown in Table 2. In these crosses there are about twice as many females as males. In Tables 6 and 7 are given the results from crosses between females heterozygous for *y* and *ls* and different kinds of males,

TABLE 3. *Offspring of all females heterozygous with respect to y ls and crossed to various males not containing ls.*
(Totals from Tables 2, 6 and 7).

	♀ ♀	♂ ♂		Total
	Total	*y*	non *y*	
Table 2	818	83	391	474
Table 6	1925	118	798	916
Table 7	16821	1585	8110	9695
Total	19564	1786	9299	11085

not containing *ls*. If the results from Tables 2, 6 and 7 are summarized we obtain (Table 3) 1786 *yellow* and 9299 non-*yellow* males. Under the previous assumption the lethality among the *yellow* males may be estimated to be

$$100(9299 - 1786)/9299 = 80{,}8\ \%.$$

Thus the lethal effect of the assumed gene seems to be about the same in both sexes, the difference being within the limits of sampling-errors.

TABLE 4. *Offspring of 2 females with y ls in one X-chromosome and Bar in the other when mated to y ls males.*

Culture number	♀♀					♂♂					Male ratio
	B	*y*	*yB*	+	Total	*B*	*y*	*yB*	+	Total	
8139	26	1	15	28	70	35	3	8	34	80	53,33
8149	29	4	9	26	68	27	8	7	23	65	48,87

In a few cases, females with *y ls* in one of the X-chromosomes have been mated to *y* males, supposed also to contain *ls* (Table 4). As was expected, here the sex-ratio is close to 50 %. Some crosses have

TABLE 5. *Offspring of 7 females with free X:s and homozygous with respect to y ls when mated to males without y ls.*

Culture number	♀♀	♂♂	Male ratio
8150	143	29	16,86
8151	103	33	24,26
8152	42	11	20,75
8153	110	45	29,03
8154	122	31	20,26
8155	142	35	19,77
8156	42	1	2,33
Total	704	185	20,81

also been made between females with free X-chromosomes and homozygous for *y ls* and males without *y ls* (Table 5). As all sons get *y ls* from their mothers a low male ratio is obtained. The low-male-producing line is kept in stock by crossing $\frac{+}{+}$ females to *y ls* males.

II. THE LOCATION OF *ls*.

The gene *ls* has been located by the aid of the genes for *white* and *prune*. Females with *y ls* in one X and *w* or *pn* in the other have been out-crossed (Tables 6 and 7). The resulting males produced from crossing-over between *y* and *w* or *pn* have been tested by mating to

females from unrelated stock having attached X-chromosomes (Tables 8 and 9).

TABLE 6. *Offspring of females with y ls B in one X-chromosome and w in the other when mated to wild type males. The figures in the brackets refer to Table 8 (italics represent culture numbers and non-italics represent number of flies).*

Culture number	♀♀	♂♂								
	Total	*w*	*yB*	*y*	*wB*	*B*	*yw*	+	*ywB*	Total
8197	175	50	5	7	32	*10218* 1				95
8198	235	50	1	5	16					72
8199	179	40	4	4	39			*10227* 1		88
10200	170	41		28	1	*10225* 1				71
10201	197	46	7	4	41			*10212* 2	*10219* 1	101
10202	231	52	3	5	49	*10213* *10217* *10224* *10226* 4		*10214* *10223* 2		115
10203	142	37	2	5	28			*10220* 1	1	74
10204	176	39	3	4	30	*10222* 1		*10228* 1		78
10205	197	43	3	11	40		*10229* 1	*10221* 1		99
10206	223	61	5	9	46	*10215* 1		*10216* 1		123
	1925	459	33	83	322	8	1	9	2	916

From Tables 6 and 8 it is evident that *ls* must lie to the left of *w*, because no *Bar* or wild-type sons contain *ls*, whereas *y w* and *y w B* males are also *ls*. When the location of *ls* is tested in relation to *pn* (Tables 7 and 9) we find that nearly all *Bar* and wild-type males give a normal sex-ratio when mated to $\frac{+}{+}$ or $\frac{y}{y}$ females. Cultures 10265 and 12149 are, however, somewhat doubtful. Here the males perhaps contain *ls*. Of the *y pn* and *y pn B* males, those used for cultures 12153 and 12157 give a very low male ratio, and these two males must have been *ls*. Culture 12150, on the other hand, has a high male ratio. Since the sons are as many as 169 the *y pn* father of this culture could hardly contain *ls* and should probably be looked upon as a case of crossing-over between *y* and *ls*. This case is, however, somewhat complicated by the fact that there is a rather small number of females in

TABLE 7. *Offspring of females with y ls in one chromosome and prune in the other when mated to wild type or prune males. The figures in the brackets refer to Table 9 (italics represent culture numbers and non-italics represent number of flies).*

Culture number	♀♀	♂♂					Culture number	♀♀	♂♂				
	Total	*pn*	*y*	*y pn*	+	Total		Total	*pn*	*y*	*y pn*	+	Total
10230	161	78	12			90							
10231	267	137	16			153	10293	128	62	14		*12142* 1	77
					10256		10294	196	95	33			128
					10264		10295	156	82	21			103
10232	210	120	33		*10265*	157	10296	204	100	50			150
					10269 4		10297	164	67	16			83
							10298	144	69	22			91
10233	204	94	26		1	121	10299	217	85	34		1	120
10234	216	101	13		*10255* 3	117	12100	207	104	24		*12141* 1	129
					10263 1	150	12101	135	50	23			73
10235	246	128	21				12102	178	70	23			93
					10262 1	180	12103	133	81	17			98
10236	235	157	22				12104	181	78	10			88
					10266 2	162	12105	188	73	2			75
10237	299	134	26				12106	129	66	5			71
10238	284	117	30			147	12107	195	99	14			113
10239	241	148	18		1	167	12108	180	74	8			82
10240	172	89	25	1		115	12109	161	69	19			88
10241	210	106	22			128						*12144* 1	
10242	207	112	28			140	12110	171	81	14			96
					10261 1	121	12111	146	80	13			93
10243	205	95	25				12112	232	117	9			126
10244	219	105	25			130	12113	181	66	15		*12146* 1	82
10245	202	113	26			139	12114	202	80	7			87
10246	172	76	16	1		93	12115	193	98	2			100
10247	277	127	28			155	12116	193	68	3			71
10248	308	147	24			171						*12145* 1	
10249	290	114	26			140	12117	169	76	6			83
10250	215	152	21			173					*12150* 1		
10251	281	144	6		*10273* 1	151	12118	168	112	21			134
				10278 1			12119	304	160	16		*12164* 1	177
10252	260	116	13			130						*12147* 2	
10253	211	111	18		*10267* 1	130	12120	199	75	5			82
							12121	190	99	5			104
					10270 1							*12156* 1	
10254	302	154	15			170	12122	235	123	33			157
10257	311	149	31			180						*12148* 1	
10258	335	133	24		*10271* 1	158	12123	214	111	28			140
							12124	165	85	26			111
					10276		12125	89	36	2			38
10259	240	91	9	*10277* 1	*10279* 2	103	12126	134	64	17			81
						141	12127	91	65	23			88
10260	246	113	28				12128	203	87	15			102
10289	134	59	18			77							
10290	155	62	26			88	12129	174	73	21	*12157* 1		95
10291	163	71	25			96							
					12143 1							*12155* 1	
10292	177	65	15			81	12130	229	113	17			131

Culture number	♀♀	♂♂					Culture number	♀♀	♂♂				
	Total	*pn*	*y*	*y pn*	+	Total		Total	*pn*	*y*	*y pn*	+	Total
12131	211	91	32			123						*12160*	
12132	195	100	22		*12154* 1	123	12137	344	151	17		*12162* 2	170
12133	168	80	20			100						*12159* *12163*	
12134	238	103	24	*12153* 1	*12149* *12151* *12152* 3	131	12138	293	133	35		*12165* 3	171
							12139	218	135	13			148
12135	192	100	23			123	12140	267	125	23	1	*12158* 1	150
12136	262	138	24			162							
							Total	16821	8067	1577	8	43	9695

culture 12150 (which also seems to be the case in some of the other cultures in Table 9). The cause of this low female ratio was not analysed, but it seems obvious that this cause must be independent of *ls*.

TABLE 8. *Males from Table 6 which are tested by crossing to* $\underline{yy}$ *or* $\underline{++}$ *females with attached X:s of unrelated stock.*

Culture number	The male from culture no.	♀♀	♂♂				Sex-ratio
		$\underline{yy}$ or $\underline{++}$	*B*	*yw*	+	*ywB*	
10212	10201	90			124		57,94
10213	10202	112	101				47,42
10214	10202	99			106		51,71
10215	10206	64	61				48,80
10216	10206	92			112		54,90
10217	10202	92	95				50,80
10218	8197	117	115				49,57
10219	10201	109				21	16,15
10220	10203	55			57		50,89
10221	10205	57			67		54,03
10222	10204	80	90				52,94
10223	10202	107			113		51,36
10224	10202	91	107				54,04
10225	10200	124	120				49,18
10226	10202	78	84				51,85
10227	8199	82			90		52,33
10228	10204	108			141		56,63
10229	10205	58		6			9,38

From these crosses it may be inferred that *ls* is located in close proximity to *y*.

We may also try to calculate the location of *ls* direct from the male offspring of a female having one X with *y ls* and the other with *w*.

TABLE 9. *Males from Table 7 which are tested by crossing to yy or ++ females with attached X:s of unrelated stock.*

Culture number	The male from culture no.	♀♀ ++ or yy	♂♂ B or +	♂♂ y pn or y pn B	Sex-ratio	Culture number	The male from culture no.	♀♀ ++ or yy	♂♂ B or +	♂♂ y pn or y pn B	Sex-ratio
10255	10234	122	128		53,33	12147	12120	89	204		69,62
10256	10232	142	151		51,54	12148	12123	69	104		60,12
10261	10243	77	76		49,67	12149	12134	172	136		44,16
10262	10236	66	68		50,75	12150	12118	60		169	73,80
10263	10235	45	62		57,94	12151	12134	160	163		50,46
10264	10232	40	61		60,40	12152	12134	135	126		48,28
10265	10232	31	22		41,51	12153	12134	143		19	11,73
10266	10237	72	113		61,08	12154	12132	125	140		52,83
10267	10253	155	172		52,60	12155	12130	144	151		51,19
10269	10232	22	47		68,12	12156	12122	100	110		52,38
10270	10254	110	106		49,07	12157	12129	107		32	23,02
10271	10258	147	142		49,13	12158	12140	139	158		53,20
10273	10251	136	176		56,41	12159	12138	78	82		51,25
10276	10259	151	134		47,02	12160	12137	84	119		58,62
10277	10259	37		24	39,34	12162	12137	138	130		48,51
10278	10252	53		38	41,76	12163	12138	98	110		52,88
10279	10259	170	211		55,38	12164	12119	27	30		52,63
12141	12100	123	136		52,51	12165	12138	148	180		54,88
12142	10293	74	82		52,56	12166	12150	33		106	76,26
12143	10292	150	163		52,08	12167	12150	27		96	78,05
12144	12110	140	151		51,89	12168	12150	51		124	70,86
12145	12117	160	175		52,24	12169	12147	49	111		69,38
12146	12113	84	111		56,92	12170	12153	311		28	8,26

The distance between *y* and *ls* is denoted by *p*, that between *ls* and *w* by *q*. Then

$$p + q = 1{,}5.$$

We further introduce the notations

	y	*w*	+	*yw*
Number of zygotes	N_1	N_2	N_3	N_4
» » hatched males	n_1	n_2	n_3	n_4

Here we may assume that $N_1 = N_2$ and $N_3 = N_4$, and as *ls* does not kill any of the *w* male zygotes we may also assume that $n_2 = N_2$. The number of *y* zygotes which have been killed by *ls* is $N_1 - n_1 = n_2 - n_1$, and the death-rate *r* is

$$r = \frac{n_2 - n_1}{N_1} = \frac{n_2 - n_1}{n_2}$$

We then find that

$$n_3 = \frac{q}{1{,}5} N_3 + \frac{p}{1{,}5}(1 - r) N_3 = \frac{1{,}5 - pr}{1{,}5} N_3$$

$$\text{and } n_4 = \frac{p}{1{,}5} N_4 + \frac{q}{1{,}5}(1 - r) N_4 = \frac{1{,}5 - qr}{1{,}5} N_4$$

or, as N_3 is assumed to be equal to N_4

$$\frac{n_3}{n_4} = \frac{1{,}5 - pr}{1{,}5 - qr}$$

Bearing in mind that $q = 1{,}5 - p$ and introducing the values $n_3 = 17$, $n_4 = 3$, obtained from Table 6, we get the result

$$p = 0{,}04.$$

In making the same calculations on the male offspring of a female having *y ls* in one X and *pn* in the other, we must take

$$p + q = 0{,}8$$

and (from Table 7) $n_3 = 43$, $n_4 = 8$
which gives

$$p = -0{,}01.$$

The conclusion to be drawn from these calculations is the same as before, i. e. that *ls* must be located very close to *y*. That the locus of *ls* is not exactly the same as that of *y* is, however, indicated by the occurrence of one probable case (culture 12150, Table 9) of crossing-over between *y* and *ls*.

SUMMARY.

1. In our material a semi-lethal gene *ls* has occurred, which kills about 80 % of the zygotes.

2. The gene *ls* is located in the X-chromosome in close proximity to *y*. Only one probable case of crossing-over between *y* and *ls* has been recorded.

3. *ls* is kept in stock in two ways:

a) low-female-producing line: $\frac{y\ ls}{y\ ls} \times B$,

b) low-male-producing line: $\frac{+\ +}{}$ × *y ls*.

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DIE ZYTOLOGIE VON ALLIUM CEPA × FISTULOSUM

VON *ALBERT LEVAN*
HILLESHÖG, LANDSKRONA, SCHWEDEN

(With a summary in English)

NEULICH haben EMSWELLER und JONES (1935 a, b) über die Morphologie und Zytologie des einzigen bisher bekannten Artbastarden von *Allium* berichtet, nämlich *Allium cepa* L. × *fistulosum* L. Dieser Bastard ist zytologisch interessant, u. a. da er die erste artifizielle Kreuzung darstellt zwischen einer Form mit zufallsmässig verteilten Chiasmata und einer mit Chiasmalokalisation. Obgleich die Fertilität des F_1-Bastarden schlecht ist, ist es EMSWELLER und JONES doch gelungen durch Rückkreuzungen zu zeigen, dass die Chiasmalokalisation als eine rezessiv mendelnde Eigenschaft vererbt wird, wodurch sie ein neues Beispiel für eine genetische Kontrolle der Meiosiseigenschaften erbracht haben.

Ohne Kenntnis der Arbeit dieser Verfasser habe ich den Bastard *A. cepa* × *fistulosum* dargestellt und auch seine Zytologie untersucht. Hierbei bin ich, soweit meine Untersuchungen mit denen von EMSWELLER und JONES parallel sind, zu ähnlichen Resultaten gekommen.

Im Sommer 1933 wurden etwa Hundert Blüten von *A. cepa* (die bekannte Handelssorte Braunschweiger) mit Pollen von *A. fistulosum* (meine Nr. 1 aus dem Botanischen Garten in Dorpat) bestäubt. Als Resultat der Kreuzung wurden 30 Samen erhalten, die im folgenden Frühjahr ausgesät wurden. 13 von diesen keimten und nach Überwinterung am Feld sind die Pflanzen auf 9 reduziert worden, die im Sommer 1935 alle blühten.

Obgleich nahestehend unterscheiden sich die beiden Elternarten in mehreren Hinsichten, wie Ausbildung der Zwiebel, Form der Blütenstände und Blüten, Zeitigkeit, Rhythmus für das Ausschlagen der Blüten in den Blütenständen u. s. w. Meistens nimmt die Hybride eine intermediäre Stellung zwischen den Eltern ein. EMSWELLER und JONES (1935 a) beschreiben ausführlich die Morphologie der Kreuzung und fügen sehr gute Abbildungen bei, weshalb ich hier nicht darauf eingehen brauche, sondern auf ihre Arbeit verweise. Eine Beobachtung in bezug auf die Pollenform sei jedoch hinzugefügt. Der Pollen war

in meinem Material von *A. cepa* bedeutend kürzer und mehr rundlich als bei *A. fistulosum*, wenn gleiche Entwicklungsstadien verglichen werden. Am Bastard wurden beide diese Pollenformen nebst Übergängen zwischen denselben beobachtet.

Die Pollenfertilität, die bei den Eltern 90—100 % guten Pollen betrug, zeigte beim Bastard das nach Meiosisstörungen typische Bild einer während der Pollenentwicklung sinkenden Fertilitätskurve. Nach der ersten Pollenteilung sank die Pollenfertilität schnell auf 2—5 % guten Pollen. Die Samenfertilität war sehr schlecht: trotz zahlreicher Selbstungen, Kreuzungen innerhalb F_1 und Rückkreuzungen wurden nur einige wenige Samen erhalten.

Im Sommer 1935 wurden Fixierungen der Elternarten und der Kreuzung vorgenommen. Es wurde die früher beschriebene zytologische Methodik verwendet (LEVAN, 1932). Die von GEITLER (1934) empfohlene Kombination von FLEMMING und BENDA erwies sich für die Fixierung der Meiosis des Bastarden vorteilhaft.

I. SOMATISCHE CHROMOSOMEN.

Die beiden Arten *A. cepa* und *fistulosum* gleichen einander in der Zahl und Form der Chromosomen. Beide haben somatisch 16 Chromosomen und bei beiden sind 14 von diesen Chromosomen mit einer medianen bis submedianen Polfadeninsertion versehen, während 2 Chromosomen (s_1) eine subterminale Insertion aufweisen. Bei beiden Arten haben die s_1-Chromosomen einen Satellit, der terminal am kürzeren Arm befestigt ist. Im folgenden werden diese s_1-Chromosomen bei *A. cepa* mit s_1c und bei *A. fistulosum* mit s_1f bezeichnet.

Es bestehen indessen zytologisch beobachtbare Unterschiede zwischen den Chromosomen der beiden Arten (Fig. 1 *a—b*). Die Chromosomen sind bei *A. cepa* grösser als bei *A. fistulosum*. Während die Chromosomen dieser letzteren Art, gemessen in der ersten Pollenmetaphase, in ihrer Länge zwischen 6—9 μ variieren, betragen die Masse für *A. cepa* 8—11 μ. Die totale Chromosomenlänge eines haploiden *fistulosum*-Kerns wurde zu 57 μ berechnet, die entsprechende Länge für *A. cepa* zu 66 μ. Auch der Chromosomendiameter ist bei *A. cepa* grösser als bei *A. fistulosum*.

Ein leicht beobachtbarer Unterschied besteht in der Ausbildung der s_1-Chromosomen (Fig. 1 *c—i*). *A. fistulosum* hat einen verhältnismässig kürzeren proximalen Arm als *A. cepa*, sein Satellit dagegen ist bedeutend grösser als der von *A. cepa*, der nur aus einer kleinen punktförmigen

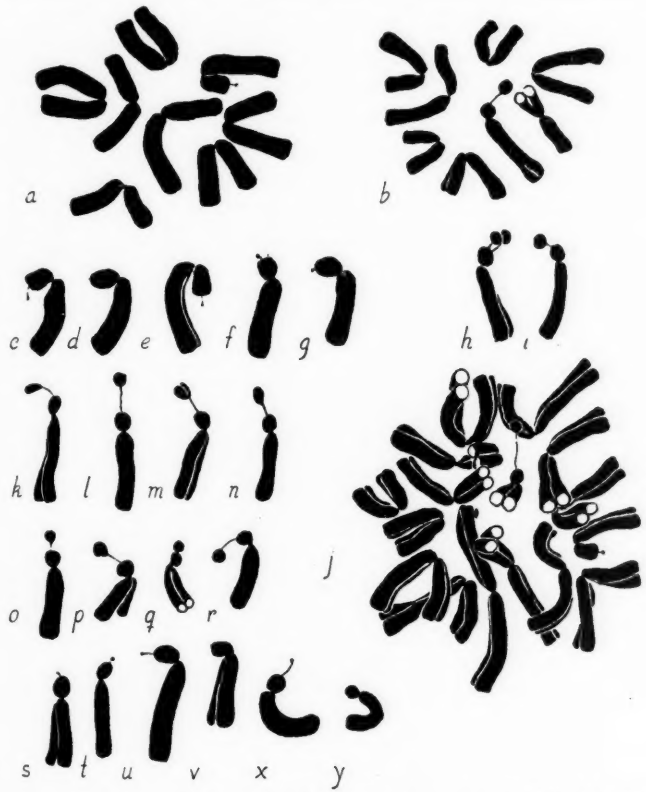

Fig. 1. *a, c—g*: *A. cepa*, *b, h—i*: *A. fistulosum*, *j—y*: *A. cepa* × *fistulosum*, *a—i*, *k—y*: erste Pollenmitose, *j*: Wurzelmitose. — × 2400.

Bildung besteht. Als Masse für die s_1-Chromosomen sind folgende berechnet worden (Mittelwerte von 5 Messungen):

	Langer Arm	Kurzer Arm	Faden + Sat.	Summe
A. cepa	4,9	1,9	0,3	7,1
A. fistulosum	4,4	1,2	1,1	6,7

Die Chromosomen des Bastarden, in Wurzelspitzen studiert (Fig. 1 *j*), bilden die Summe der Gametenchromosomen der Eltern. Sowohl s_1c wie s_1f können identifiziert werden. Alle Chromosomen in der gleichen Platte haben gleichen Chromosomendiameter; ob die *A. cepa*-Chromosomen auch hier länger sind lässt sich nicht entscheiden.

Der Chromosomendiameter des Bastarden scheint zwischen jenen der Eltern intermediär zu sein. Fig. 1 *k—y* zeigen eine Anzahl s_1-Chromosomen, gezeichnet aus Pollenkörnern des Bastarden. Wie ersichtlich kommen sowohl s_1c wie s_1f mit normaler Form vor.

II. MEIOSIS.

Die Meiosis von *A. fistulosum* ist früher in ihren Einzelheiten beschrieben worden (LEVAN, 1933). Sie wird durch eine ausgeprägte Lokalisation der Chiasmata charakterisiert, die zur Entstehung von 8 cruciformen Gemini führt. *A. cepa* dagegen folgt das für *Allium* ge-

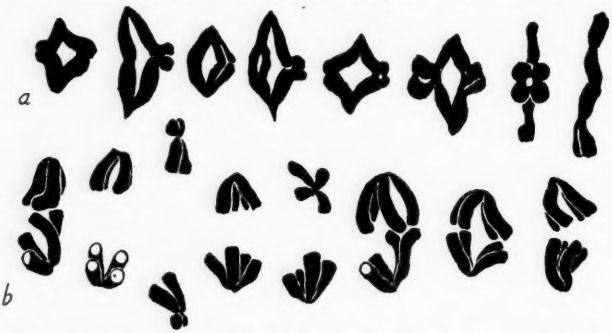

Fig. 2. *A. cepa*, *a*: erste Metaphase, *b*: erste Anaphase. — × 2400.

wöhnliche Schema der Meiosis mit zufallsmässiger Verteilung der Chiasmata. Es werden 8 ring- oder stabförmige Gemini gebildet (Fig. 2 *a*, *b*). Für 5 analysierte Metaphasenplatten wurden für die Chiasmazahl bei *A. cepa* folgende Werte erhalten:

Anzahl xx per II:	1	2	3	Summe xx	Summe Term. xx
Anzahl Fälle:	10	26	4	74	30

Die Meiosis des Bastarden wird dadurch charakterisiert, dass die von den Eltern erhaltenen Chromosomen allerdings im grossen paarweise homolog, aber doch so verschieden sind, dass zahlreiche Hybridenstörungen entstehen. Wie schon erwähnt worden ist, dominiert in F_1 die zufallsmässige Verteilung der Chiasmata, weshalb der Bastard in bezug auf die Meiosis am ehesten mit *A. cepa* verglichen werden kann.

Von den Prostadien beim Bastard habe ich nur die Pachytäne näher untersucht, die ein sehr charakteristisches Bild aufweist. In Fig. 3 sind einige Pachytänechromosomen abgebildet, die einige der

beobachteten Abnormitäten zeigen. Ungepaarte Fäden kommen zahlreich im ganzen Pachytänestadium vor, in weit auffallenderem Grad als dies beispielsweise bei autotriploiden Formen von *Allium* der Fall ist. Häufig paaren sich 2 verschiedene Teile eines Chromosomenpaares, während dazwischenliegende Teile ungepaart verbleiben, zuweilen paaren sich verschiedene Regionen des gleichen Chromosoms mit 2 verschiedenen Chromosomen, mitunter, jedoch seltener, schien ein Teil

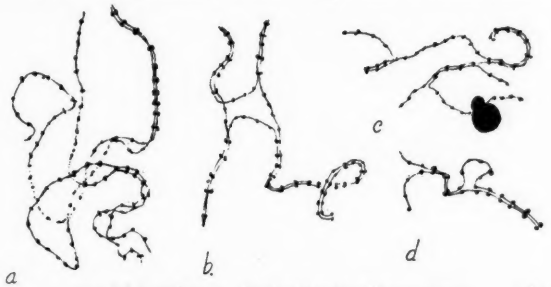

Fig. 3. *A. cepa* × *fistulosum*, Pachytänekonfigurationen. — × 2400.

eines Chromosoms sich mit einem anderen Teil des gleichen Chromosoms zu paaren. Es liegen also viele Zeichen für strukturelle Verschiedenheiten zwischen den beiden Elterngenomen vor.

Mit diesen Voraussetzungen soll die Metaphase I Störungen ausgesetzt sein. Dem folgenden Bericht über dieses Stadium liegt u. a. eine Analyse von 100 Zellen von 3 Präparaten zweier Bastardpflanzen zugrunde, deren Zytologie ganz übereinstimmen scheint.

Ausser Bivalente kommen Univalente und Assoziationen von mehr als 2 Chromosomen vor, die im folgenden der Einfachheit halber oft Trivalente, Quadrivalente u.s.w. genannt werden. Die Konfigurationen werden auch mit römischen Zahlen bezeichnet. In 100 Zellen zeigten die Chromosomen folgende Konfigurationen:

Konfiguration					Anzahl Fälle	Konfiguration					Anzahl Fälle
I	II	III	IV	VI		I	II	III	IV	VI	
0	8	—	—	—	8	4	3	—	—	1	1
1	6	1	—	—	5	5	4	1	—	—	3
2	7	—	—	—	26	6	5	—	—	—	18
2	6	—	1	—	1	8	4	—	—	—	6
3	5	1	—	—	6	10	3	—	—	—	3
4	6	—	—	—	19	12	2	—	—	—	1
4	4	—	1	—	3	Summe: 380 I, 578 II, 14 III, 4 IV, 1 VI					

Der auffallendste Unterschied zwischen der Meiosis des Bastarden und den Verhältnissen bei *A. cepa* besteht im Zusammenhang mit der Chiasmaanzahl per Zelle. In 100 Zellen wurden beim Bastard folgende Zahlen erhalten:

Anzahl xx per Zelle:	2	3	4	5	6	7	8	9	10	11	$M \frac{xx}{Zelle}$
Anzahl Fälle: ...	1	2	3	5	9	20	23	21	13	3	7,75

Während der Bastard also etwa 7,8 Chiasmata per Zelle hatte, zeigte *A. cepa* fast die doppelte Anzahl, nämlich 14,8. *A. fistulosum*, wegen der Chiasmalokalisation nicht vergleichbar, hatte 16,8 Chiasmata per Zelle.

Die Anzahl terminaler Chiasmata per Zelle sind beim Bastard folgende:

Anzahl term. xx per Zelle:	0	1	2	3	4	5	$M \frac{term.\ xx}{Zelle}$	Term. Koeff.
Anzahl Fälle:	4	24	40	18	11	3	2,17	0,280

Die Terminalisation ist bei *A. cepa* bedeutend grösser (Term. Koeff. 0,405), was mit dem grösseren % ringförmiger Bivalente im Zusammenhang stehen kann, aber sicherlich auch auf »changes in homology« beruht, die beim Bastard die Terminalisation hindern. *A. fistulosum* dagegen hat nur in seltenen Ausnahmefällen ein terminales Chiasma.

Univalente kommen beim Bastard zahlreich vor. In 100 Zellen wurde folgende Frequenz gefunden:

Anzahl I per Zelle:	0	1	2	3	4	5	6	7	8	9	10	11	12	M I/Zelle
Anzahl Fälle: ...	8	5	27	6	24	3	17	0	6	0	3	0	1	3,8

Dass Zellen mit einer geraden Anzahl Univalente häufiger sind als mit einer ungeraden beruht darauf, dass eine ungerade Anzahl nur im Zusammenhang mit der Bildung eines Trivalents oder einer höheren Konfiguration entsteht, während eine ausgebliebene Chiasmabildung bei der weit häufigeren Bivalentpaarung zu einer geraden Anzahl von Univalenten führt. Auf Grund der Lage der Univalente in der Metaphasenplatte kann man häufig darauf schliessen, dass sie infolge mangelhafter Chiasmabildung innerhalb gepaarten Chromosomen entstanden sind.

Die Univalentform ist die bei *Allium* gewöhnliche, die Insertionseinschnürung ist vollkommen sichtbar, und die Chromosomen nehmen die für somatische Chromosomen charakteristische Form an, die Kontraktion ist jedoch grösser als in somatischen Zellen. Zuweilen konnten unter den Univalenten s_1c und s_1f erkannt werden (Fig. 4 *b*). Auch in diesem Stadium sind ihre Satelliten vollkommen sichtbar.

Die Bivalente des Bastarden sind zufolge der geringen Chiasmaanzahl per Zelle gewöhnlich stabförmig. In 100 Zellen wurden für die Bivalente folgende Chiasmazahlen erhalten:

Anzahl xx:	1	2	3	Summe Fälle	M xx/II
Anzahl Fälle:	443	126	9	578	1,25

Das Aussehen der Bivalente beim Bastard geht aus Fig. 4 *a*—*i* hervor. Sie sind häufig, wahrscheinlich immer, asymmetrisch. Mitunter ist der Grössenunterschied und der Formunterschied innerhalb eines Bivalents sehr auffallend. Vielemale konnte ich mit Sicherheit feststellen, dass alle 4 Chromosomenteile um ein Chiasma in verschiedener Weise ausgebildet waren, entweder hinsichtlich Länge, Platz für die Polfadeninsertion, Vorkommen von Satelliten oder dgl. Solche Fälle besitzen theoretische Bedeutung für die Deutung des Verhaltens der Chiasmata zum Crossing-over.

In ein paar einzelnen Fällen (2 von 100 Zellen) gab es eine Paarungsabnormität in den Bivalenten, indem das eine Chromosom ein Chiasma mit einem anderen Teil des gleichen Chromosoms ausgebildet hatte, wobei ein kleiner Ring entstand (Fig. 4 *p*).

Von höheren Chromosomenkomplexen als Bivalente gab es Assoziationen von 3—6 Chromosomen. Von diesen waren Trivalente am häufigsten. Diese zeigten oft einfachen Typus, Kette von drei, Ring und Stab (Fig. 4 *j*—*m*). Ein paar Fälle von 3 Stäben, in einem Punkt mit einem triple-Chiasma vereinigt, wurden auch beobachtet (Fig. 4 *n*, *o*). Hierbei war zu sehen, dass ein Chromosom verschiedene Grösse und Aussehen hatte als die beiden übrigen. Die Trivalente hatten 2—4 Chiasmata. Ein Quadrivalent vom Kettentypus mit 3 Chiasmata zeigt Fig. 4 *q*. Eine Assoziation von 6 Chromosomen wurde nur einmal beobachtet (Fig. 4 *b*).

Die Anaphase I verläuft sehr unregelmässig. Die Separation der Chromosomen, die nach verschiedenen Polen wandern, ist häufig »unrein». Chromatinbrücken zwischen den Polen sind ganz sicher oft dadurch bedingt, dass die Terminalisation der Chiasmata durch

»changes in homology» zwischen den Chromatiden verhindert wird. So sieht man häufig ein interstitielles Chiasma in der Mitte einer zwischen

Fig. 4. *A. cepa* × *fistulosum*, erste Metaphase, *a—b*: Chromosomen ganzer Zellen, *c—l*, *p*: asymmetrische Bivalente, *j—o*: Trivalente, *q*: Quadrivalent. — × 2400.

beiden Polen ausgespannten Chromatinbrücke sitzen. In anderen Fällen liegt ein kleines loses Fragment in der Nähe der Chromatinbrücke

häufig in der Äquatorebene, und dann kann man mit Recht die Anwesenheit eines Chromosoms mit 2 Insertionen vermuten, die je nach einem Pol gewandert sind. Die Univalente wandern in der späten Anaphase zum Äquator hinein und bilden eine sekundäre Metaphasenplatte ähnlich wie bei gewissen Triploiden. Sie werden häufig in der ersten Teilung geteilt, aber sie kommen beim Einschluss in die grossen Telophasenkerne oft nicht mit.

Die Interkinese wird durch eine grosse Anzahl Mikronuclei charakterisiert. In einem Präparat wurden solche in folgender Anzahl gefunden:

Anzahl Mikronuclei:	1	2	3	4	5	6	7	8	M
Anzahl Fälle:	1	7	11	9	6	2	2	1	3,54

Auch die zweite Teilung ist vielen Störungen ausgesetzt. In einer zweiten Telophase wurde folgende Anzahl extra Kerne gezählt:

Anzahl Mikronuclei:	0	1	2	3	4	5	M
Anzahl Fälle:.....	12	18	12	5	2	1	1,40

III. DIE POLLENENTWICKLUNG.

Wie auf Grund der nun beschriebenen Störungen und Abnormitäten während der Meiosis im Bastard zu erwarten ist, findet man im Pollen sehr grosse Unregelmässigkeiten. In der Tat gleicht die Pollenentwicklung bei diesem Bastard in vielem der Pollenentwicklung, die nach einer starken Bestrahlungsreizung der Meiosis erhalten wird. Es zeigt sich also, dass die Hybridität einen ähnlichen Effekt wie Röntgenbestrahlung hervorrufen kann. Gleichwie bei der Beschreibung der Röntgenwirkung auf *Allium Schoenoprasum* (LEVAN, 1936) ist es zweckmässig die Beschreibung der Hybridwirkung in Zellenanomalien und Chromosomenanomalien aufzuteilen.

1. ZELLENANOMALIEN.

Die Pollenkörner, die bei den Eltern in bezug auf Grösse und Form gleichmässig sind, zeigen beim Bastarden ein mannigfaltiges Aussehen, von grossen Riesenkörnern mit kugelförmiger Gestalt bis zu kleinen Mikrozyten; die ersteren als Resultat von Vereinigungen aller 4 Zellen

in einer Tetrade, letztere die Reste von vielleicht nur einem einzigen Chromosom enthaltend.

Meiosisanomalien, die vor allem zu Störungen der Zellenbildung im Pollen disponieren, sind persistierende Chromosomenbrücken, die die

Fig. 5. *A. cepa* × *fistulosum*, zwei abnorme Pollenkörner, *a*: 6, *b*: 18 Chromosomen. — × 2400.

vollständige Wandbildung zwischen den Tetraden verhindern, sowie vagabundierende Chromosomen, bzw. Chromosomenfragmente, die häufig in kleinen akzessorischen Zellen eingeschlossen werden, zuweilen durch einen Kanal an grösseren Zellen festhängend (Fig. 5 *a*).

Gigaspollenkörner mit einer Chromosomenzahl von oder an-

nähernd der somatischen Zahl waren in den Hybridenpflanzen sehr häufig. Sie hatten verschiedene Entstehungsweise. Bei drei der Hybridenpflanzen gab es Gigaspollenkörner in einem regelmässigen, hohen % (20—30 %). Sie waren in diesen Fällen ganz sicher genetisch bedingt, entstanden durch die in *Allium* so gewöhnliche monokinetische Meiosis. In übrigen Fällen dürften die Gigaspollenkörner durch Störungen in der ersten oder zweiten meiotischen Teilung verursacht worden sein. In einigen Fällen konnte man diese Störungen direkt auf eine mangelhafte Wandbildung in einer der Teilungen und einer Kernverschmelzung zurückführen. So verhält es sich mit dem in Fig. 5 *b* abgebildeten Pollenkorn, wo die Wand teilweise gebildet worden ist. In einem anderen hier nicht abgebildeten Fall ist die Wand fast vollständig gebildet worden und hat nur einen feinen Kanal übrig gelassen (ca. 1,5 μ Diameter). In der einen Hälfte gab es keine Spur eines Zellenkerns, in der anderen befand sich der Kern gerade in Teilung und zeigte 16 Chromosomen. Offenbar ist der eine Tetradenkern in der einen oder anderen Weise in die Schwesterzelle hineintransportiert worden und dort mit dem zweiten Kern verschmolzen.

2. CHROMOSOMENANOMALIEN.

Infolge der grossen und während der Pollenentwicklung zunehmenden Pollensterilität beim Bastard war es recht schwierig die Chromosomen im Pollenkorn zu studieren. Gewöhnlich gab es in jedem Präparat nur einige wenige vitale Zellen mit den Chromosomen in zur Beobachtung geeigneten Stadien. Folgende Daten gründen sich auf Untersuchung von 92 Präparaten (Pollen von 46 Blüten enthaltend) und in diesen befanden sich zusammen nur 59 Zellen in typischer Pollenmetaphase. Zum Vergleich sei erwähnt, dass bei *Allium* gewöhnlich ein einziges Präparat Hunderte von guten Metaphasenplatten enthalten zu pflegt.

Die untersuchten Zellen, darunter 10 Gigaszellen, zeigten folgende Chromosomenzahlenverteilung:

Chromosomenzahl:	4	5	6	7	8	9	10	11	12—15	16	17	18	19	Summe
Anzahl Zellen:...	1	0	3	4	23	14	2	2	0	6	1	2	1	59

Bei Ausschluss der Gigaspollenkörner gibt dies einen Mittelwert für die Chromosomenzahl des Pollens von 8,06. Die Meiosisstörungen haben eine starke Wirkung auf die zahlenmässige Verteilung der Chromoso-

men auf die verschiedenen Tetradenzellen gehabt. Bei den Elternarten ist (abgesehen von einzelnen Gigaspollenkörnern mit 16 Chromosomen) nicht ein einziges Pollenkorn mit einer anderen Chromosomenanzahl als 8 beobachtet worden, hier beim Bastard variieren die Chromosomenzahlen von 4—19.

Am wenigsten erwartet waren die Pollenkörner, bei denen die Chromosomenzahl unter der haploiden Zahl lag. In allen früher untersuchten *Allium*-Arten werden schon vor der ersten Pollenteilung jene Zellen zurückgebildet, denen ein Chromosom der Grundgarnitur fehlt (bei *A. Schoenoprasum* wurde jedoch einmal eine weit vorgeschrittene Pollenprophase mit 7 Chromosomen beobachtet). Sämtliche in obenstehender Tabelle aufgenommenen Pollenkörner waren in ihrem Aussehen normal und befanden sich in normaler Teilung. Das vierchromosomige Pollenkorn enthielt ausser den Chromosomen einen Chromatinklumpen (Fig. 6 *e*). In 18 Fällen hatten die Pollenkörner 1—3 Extrachromosomen ausser der haploiden Zahl. In diesen gleichwie in den 8-chromosomigen Pollenkörnern besteht jedoch keine Sicherheit dafür, dass nicht gewisse Chromosomen der Basalgarnitur fehlen. In einigen Fällen konnte dies in bezug auf das einzige morphologisch identifizierbare Chromosom s_1 direkt gezeigt werden.

Die Chromosomenzahl ist indessen nicht der einzige Faktor, der im Bastardpollen variiert, dies ist auch mit dem morphologischen Aufbau der Chromosomen der Fall. Die Variation, die sich zytologisch in der Form von Aberrationen in der Chromosomenmorphologie äussert, d. h. in der Anwesenheit von »neuen» Chromosomentypen, kann auf strukturelle Umlagerungen in der Chromatinsubstanz zurückgeführt werden, die in der einen oder anderen Weise in der Meiosis stattgefunden haben. Meistens handelt es sich um Fragmentationen und Translokationen.

In der Meiosis des Bastarden treten, wie früher erwähnt worden ist, namentlich in der ersten Anaphase eine grosse Menge von Chromosomenfragmenten auf. In der Pollenteilung sind Fragmente nicht so häufig, was bedeutet, dass die Fragmente nach ihrer Bildung meistens bald atrophiert werden. In einigen Fällen kommen jedoch Fragmente in der ersten Pollenteilung vor und verhalten sich wie normale Chromosomen. Sie sind dann stets mit einer eigenen Insertionseinschnürung versehen (Fig. 6 *a*, *x*).

Chromosomen mit an einem Faden angehefteten terminalen oder lateralen Fragmenten sind ziemlich häufig. Fig. 5 *a*, *b* und Fig. 6 *f*, *h*, *r*, *t* bilden Beispiele hierfür. Zuweilen gibt es lateral angeheftete, oft

paarige Bildungen, die so klein sind, dass sie s_1c-Satelliten gleichen (Fig. 6 *a*, *i*). In diesem Zusammenhang sei auf SWEZY (1935) verwiesen,

Fig. 6. *A. cepa* × *fistulosum*, erste Pollenmetaphase, *a*—*e*: Chromosomen ganzer Pollenkörner, *a*: 19, *b*: 17, *c*: 7, *d*: 9, *e*: 4 Chromosomen, *f*—*y*: einzelne abnorme Chromosomen. — × 2400.

der eine ausgedehnte Variation in der Plazierung der Satelliten in somatischen Zellen ein und derselben *Crepis*-Pflanze gefunden hat.

Die häufigsten strukturellen Chromosomenveränderungen im Bastardpollen sind doch ganz sicher einfache Umlagerungen des Chro-

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Die häufigsten strukturellen Chromosomenveränderungen im Bastardpollen sind doch ganz sicher einfache Umlagerungen des Chro-

matins. Solche werden nur entdeckt, wenn die herbeigeführten Veränderungen in den Proportionen der Chromosomen so gross sind, dass sie direkt beobachtet werden können, oder wenn ein Chromosomenarm mit einem Satelliten davon betroffen wird. Im Falle *A. cepa* × *fistulosum*, wo alle Chromosomen ausser s_1 median—submedian eingeschnürt sind, werden am leichtesten Veränderungen entdeckt, die zur Entstehung von subterminal oder terminal inserierten Chromosomen geführt haben, aber auch submedian inserierte Chromosomen mit Armen von ungewöhnlich grosser Länge können beobachtet werden. Derartige Chromosomenformen bilden u. a. Fig. 6 *g*, *j*—*l*, *o*, *v*, *y*. Gerade dieser Typus von hybridogenen Chromosomenveränderungen dürfte von allen beobachteten Typen derjenige sein, der vom Standpunkte der Evolution die grösste Bedeutung hat.

Seltener treten Chromosomen mit 2 Polfadeninsertionen auf (Fig. 6 *b*, *m*, *u*) und ein ringförmiges Chromosom wurde nur einmal beobachtet (Fig. 6 *c*).

Die Gigaspollenkörner enthalten ähnliche Abweichungen im Chromosomentypus wie die normalen Pollenkörner (Fig. 5 *b*, 6 *a*, *b*). Zuweilen legt die paarweise Anordnung der Chromosomen nahe, dass eine monokinetische Meiosis stattgefunden hat. Hierbei ist zu beachten, dass zwischen den Komponenten solcher Paare häufig morphologische Unterschiede vorhanden sind; ganz natürlich, da ja bei dieser Meiosisform ein normales Crossing-over vorkommt. Da der gleiche Chromosomenarm gewöhnlich von höchstens einem Chiasma getroffen wird, sollen innerhalb eines heteromorphen Paars gerade bei der zweiten Teilung verschiedene Chromatiden getrennt werden, und in der monokinetischen Meiosis wird diese Teilung unterdrückt.

Der Chromosomendiameter zeigt beim Bastardpollen eine erheblich grössere Variation zwischen verschiedenen Pollenzellen, als was bei *Allium* gewöhnlich der Fall ist. Ich hebe besonders die grosse Variation im Diameter der s_1-Chromosomen in Fig. 1 *k* –*y* hervor. Hierbei liegt vielleicht der Gedanke am nächsten zur Hand, dass eine ungleiche Vitalität bei verschiedenen Chromosomenkombinationen eine verschiedene Wirkung des Fixiermittels bedingt. Vielleicht handelt es sich indessen um eine Spaltung von genetischen Faktoren für Chromosomenbreite. Selten werden die Grenzen erreicht, die die Chromosomenbreiten der Elternarten bilden, was andeutet, dass es mehrere Faktoren für Chromosomenbreite, lokalisiert in verschiedenen Chromosomen, gibt.

IV. DISKUSSION.

Wenn ein Bastard gebildet wird, bekommt er die Summe der Gametenchromosomen der Elternformen. Bei mehreren Gelegenheiten hat man zeigen können, dass dies nicht nur für die Chromosomenzahl selbst gilt, sondern auch für Form und Eigenschaften jedes individuellen Chromosoms. Indessen gibt es eine gewisse Reaktion der Chromosomen gegen das neue Milieu, das sie im Zusammenhang mit der Bastardierung erhalten. Hierher gehört das Phänomen, das man bei *Crepis* gefunden und Amphiplastie genannt hat (NAVASHIN, 1930). Dieses gibt sich dadurch kund, dass gewisse Satelliten beim Bastard unsichtbar werden. Laut DARLINGTON (1932 b) bedeutet dies einen Unterschied in der Reaktion der Eltern und des Bastarden gegen Chromosomenkonstriktionen. Beim *Allium*-Bastard gab es keine Amphiplastie, sondern beide Satelliten waren sowohl in Wurzelzellen wie während der Gametogenesis sichtbar. Dasselbe ist der Fall in anderen untersuchten Bastarden. In bezug auf *Iris* schreibt SIMONET (1934): »Même les configurations les plus délicates des chromosomes (satellites et constrictions) gardent leur entière individualité dans les cinèses de l'hybride» (l. c. S. 351).

Eine andere Chromosomeneigenschaft, die man bei Eltern und Bastarden häufig verschieden findet, ist der Chromosomendiameter. Gewöhnlich bekommt, gleichwie bei *Allium*, der Bastard in seinen somatischen Teilungen eine einheitliche Chromosomenbreite. So verhält sich *Crepis* (NAVASHIN, 1931): »The present writer has made a large number of comparative observations in F_1 interspecific hybrids (1929), and it was found that the parental chromosomes never differ in width in hybrids, even though they previously displayed marked differences in the pure species» (l. c. S. 224). Ein *Iris*-Bastard *Iris* × *Paltec* verhielt sich ganz gleich wie *Allium* (SIMONET, 1931). Von den Eltern hatte *Iris pallida* bedeutend grössere Chromosomen, sowohl in bezug auf Länge und Breite, als *Iris tectorum*. Die Chromosomen des Hybriden dagegen hatten einheitlichen Diameter und intermediäre Grösse zwischen jenen der Eltern.

Eine im Bastard noch vorhandene Differenz im Diameter der Elternchromosomen konnte jedoch zuweilen beobachtet werden. Dies ist der Fall bei dem bekannten amphidiploiden Bastard *Aesculus carnea* (SKOVSTED, 1929). DARLINGTON hat mit Hinblick auf diesen eigentümlichen Fall eine Theorie von akzessorischen Substanzen in den Chromosomen aufgestellt, die also nebst genetischen und strukturellen

Faktoren das Aussehen der Chromosomen bestimmen sollten. Auch gewisse *Gossypium*-Bastarden zeigen verschiedene Chromosomendiameter innerhalb der gleichen Zelle (SKOVSTED, 1934, 1935). So hat beispielsweise *Gossypium Davidsonii* somatisch 26 kleine Chromosomen, während *Gossypium Sturtii* 26 bedeutend grössere hat. In somatischen Zellen des Bastarden gibt es 13 Chromosomen jeder Art, die sich also durch Länge und Breite unterscheiden.

Die Meiosis von Artbastarden zeigt eine bunte Mannigfaltigkeit von Typen. So gibt es z. B. alle möglichen Übergänge zwischen einer vollkommen regelmässigen Meiosis mit vollkommener Paarung und sogar gleich hoher Chiasmaanzahl wie bei den Eltern bis zu ganz mangelhafter Paarung, wobei alle Chromosomen in der Form von Univalenten auftreten. Hierbei besteht keine regelmässige Korrelation zwischen guter Meiosispaarung und systematischer Verwandtschaft.

DARLINGTONs Theorie der Meiosis macht die Chromosomenpaarung in der Metaphase I ganz und gar vom Vorhandensein von Chiasmata abhängig. Diese entstehen in gepaarten Teilen der Pachytänebivalente. Die Paarung in der Pachytäne ist also hierbei der ausschlaggebende Faktor. Wenn man von Fällen von nicht homologer Paarung absieht, die MATHER (1935) als »ineffective» beurteilt hat, muss die Pachytänepaarung auf eine Attraktion zwischen identischen Chromosomenteilen zurückgeführt werden. Mangelhafte Paarung entsteht teils zufolge struktureller Ursachen, wie Verschiedenheiten in Material oder Anordnung von Chromosomenteilen, teils zufolge faktorieller Ursachen, deren Wirkung ziemlich vollständig (Asynapsisgene) oder so schwach sein kann, dass sie nur durch statistische Untersuchungen nachweisbar ist (PETO, 1933).

Es zeigte sich, dass die schlechte Meiosispaarung bei *A. cepa* × *fistulosum* im Zusammenhang stand mit der bedeutend niedrigeren Chiasmazahl des Bastarden im Vergleich mit den Eltern, was sich im Auftreten von Univalenten und einer grösseren Anzahl von stabförmigen Bivalenten im Verhältnis zu ringförmigen als bei *A. cepa* äusserte. Erwähnt sei dass der von EMSWELLER und JONES dargestellte Bastard in der Meiosis ein viel regelmässigeres Verhalten zeigt als der hier beschriebene. In 94 Zellen von 130 gab es in der Metaphase I vollkommene Bivalentpaarung und eine höhere Anzahl Univalente als 4 kam nur in 3 Fällen vor. Ferner wurden niemals Assoziationen von mehr als 2 Chromosomen beobachtet. Die Anzahl von Chiasmata per Zelle war nach den Abbildungen (l. c. Plate 6) zu urteilen bedeutend grösser als in dem hier beschriebenen Bastard, und in den beiden photo-

graphierten vollständigen Platten gab es mehrere ringförmige Bivalente. Dies deutet an, dass die Elternformen in den Kreuzungen von EMSWELLER und JONES weniger voneinander abgewichen sind als die beiden von mir benutzten. Gewisse Verschiedenheiten in der Chromosomenmorphologie zwischen ihren Elternformen und den hier beschriebenen zeigen in die gleiche Richtung.

Eine niedrigere Chiasmaanzahl beim Bastard im Verhältnis zu den Eltern ist durch Chiasmazählungen nachgewiesen worden u. a. bei *Triticum* (DARLINGTON, 1931; MATHER, 1935) und *Gossypium* (SKOVSTED, 1935). Rein qualitativ geht indessen die niedrigere Chiasmaanzahl bei Bastarden durch das Vorkommen von Univalenten hervor, die in der Tat das auffallendste Charakteristikum für Bastarde bilden (vgl. zusammenfassende Tabellen in BLEIER, 1934).

Die strukturellen Unterschiede zwischen den Elternchromosomen äussern sich im Bastard u. a. durch die Entstehung von asymmetrischen Bivalenten und im Auftreten von höheren Chromosomenbindungen als auf Grund der Anzahl vorhandener Chromosomensätze zu erwarten gewesen wäre. Asymmetrische Bivalente sind bei Bastarden in mehreren Pflanzengattungen konstatiert worden und im allgemeinen sind sie als ein Beweis für Allosyndese aufgefasst worden. Beispiele für Pflanzengattungen mit heteromorphen Bivalenten sind *Ribes* (MEURMAN, 1928), *Crepis* (AVERY, 1930), *Lycopersicum* (LINDSTROM und HUMPHREY, 1933) und *Triticum* (MATHER, 1935). Die Asymmetrie wird durch verschiedene Umstände bedingt, verschiedene Länge der beiden Komponentenchromosomen, verschiedene Lage der Paarungszone oder beide diese Erscheinungen zusammen. Von theoretischem Interesse sind, wie früher betont worden ist, die sowohl von EMSWELLER und JONES (1935 b) wie in dieser Untersuchung in grosser Menge angetroffenen Bivalente, die ein interstitielles Chiasma, umgeben von vier Chromosomenteilen haben, die alle verschiedene Länge aufweisen. Schöne Beispiele hierfür bilden EMSWELLER und JONES' Abbildungen auf Plate 6 b, das erste und sechste Bivalent. Fig. 4 *c—i* in vorliegender Arbeit sind Beispiele für die gleiche Erscheinung. Nach solchen Bildungen hat DARLINGTON (beispw. 1932 a, S. 264) früher gefahndet, aber wie er neulich mitgeteilt hat (1935, S. 194), sind sie erst jetzt von verschiedenen Forschern in diversen strukturellen Hybriden aufgefunden worden. Die grosse Bedeutung, die einer sicheren Feststellung dieser vierfach asymmetrischen Bivalente und einem direkten Nachweis des Chromatidenaustausches im vorhandenen Chiasma beigemessen wird, hat ihren Grund darin, dass derartige Chiasmata durch Crossing-over

gebildet worden sein müssen. Sie können also nicht laut der »klassischen» Chiasmatypiehypothese erklärt werden und bilden den einfachsten Beweis für DARLINGTONS »Neo-Chiasmatypiehypothese».

Die Anaphasenseparation von heteromorphen Bivalenten kann entweder reduktionell oder äquationell sein. Entscheidend hierbei ist welche Anzahl von Chiasmata zwischen Polfadeninsertion und dem Chromosomenende gebildet werden. Bei einer ungeraden Anzahl wird die erste Anaphase reduktionell, bei Null oder einer geraden Anzahl äquationell. Da bei *Allium* selten mehr als ein Chiasma per Arm auftritt, sieht man, dass meistens ein langes und ein kurzes Ende zum gleichen Pol geht.

Die asymmetrische Paarung mit darauffolgendem Crossing-over veranlasst eine Umrangierung des vorhandenen Chromatins im Verhältnis zu den Polfadeninsertionen. Da diese Art von Chromosomenveränderungen schon vorhandene strukturelle Unterschiede zwischen den Chromosomen voraussetzen, bezeichnet DARLINGTON diese als sekundäre strukturelle Veränderungen zum Unterschied von z. B. durch Bestrahlungen induzierten Veränderungen, die primäre genannt werden. Durch »unequal crossing-over» können neue stabile Chromosomentypen entstehen, entweder direkt oder via der Entstehung von Chromosomen mit zwei Polfadeninsertionen, die dann bei einer Mitose an irgend einer Stelle zwischen den Polfadeninsertionen geteilt werden. Dieser letztere Mechanismus ist stets von einer Freimachung eines Chromosomenstückes ohne Polfadeninsertion begleitet. Er ist namentlich bei Heterozygotie für invertierte Segmente sehr plausibel und ist u. a. von MC CLINTOCK (1931), MÜNTZING (1934) und SMITH (1935) angenommen worden. In diesem letzten Fall zeigt der Verfasser, dass es nicht direkt auf dem Zufall beruht, ob beide Polfadeninsertionen bei der ersten Teilung nach dem gleichen oder nach verschiedenen Polen gehen, sondern dass dies vom Vorkommen eines Chiasmas zwischen den Polfadeninsertionen und der Invertion abhängt, weshalb die eine Verteilung viel häufiger ist als die andere.

Die Entstehung von neuen Chromosomentypen durch Crossing-over in Artbastarden hat man bei ein paar Gelegenheiten beobachtet. So traten unter den Nachkommen von Artbastarden von *Crepis* bei zwei Gelegenheiten morphologisch neue Chromosomentypen auf (NAVASHIN, 1927; HOLLINGSHEAD, 1930). In beiden Fällen handelte es sich um ein verkürztes Chromosom, das in den Nachkommen eines triploiden Artbastards angetroffen worden ist. In Nachkommen von Hybriden zwischen Arten innerhalb *Vicia* conspecies *sativa* traten neue Chromosomen-

typen auf (SWESHNIKOWA, 1932). Die Verfasserin schreibt: »It was established that besides roentgenization hybridization may serve also as a source of translocations».

Dass man gleichwie im Bastard zwischen *Allium cepa* und *fistulosum* schon bei der ersten Pollenteilung des Bastarden direkt die durch Crossing-over entstandenen neuen Chromosomentypen beobachten kann, dürfte recht ungewöhnlich sein.

SUMMARY.

The cytology of the bastard *Allium cepa* × *fistulosum* is described.

The origin of new chromosome types by unequal crossing-over is demonstrated.

Hilleshög, im November 1935.

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DIE REDUKTIONSTEILUNG IN EINIGEN ARTBASTARDEN VON PISUM

VON *ARTUR HÄKANSSON*
LUND

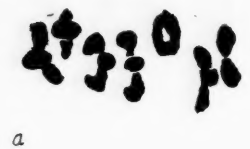
(With a summary in English)

DANK dem grossen Entgegenkommen von Dr. H. DE HAAN, Wageningen, Holland, habe ich Samen von mehreren Artbastarden von *Pisum*, die von ihm hergestellt wurden, erhalten. Diese Samen hatte ich im Jahre 1934 ausgesäht und konnte Fixierungen von verschiedenen Pflanzen machen. Wenn auch die Zytologie von *Pisum* viel studiert worden ist, sind doch die Chromosomenverhältnisse in den Artbastarden wenig bekannt. Die Zytologie von *Pisum humile* × *P. sativum* ist indessen untersucht (LUTKOV). Der Bastard hatte nach LUTKOV dieselbe Chromosomenzahl wie die Elternarten ($2n = 14$), seine Reduktionsteilung ist ganz normal mit sieben Bivalenten in der Metaphase I. Trotz der regelmässigen Reduktionsteilung ist der Pollen des F_1-Bastards doch ziemlich schlecht, indem nur etwa 40 % der Körner ein normales Aussehen hatten, die anderen waren abortiv. Von den anscheinend normalen Körnern konnte nur eine kleine Anzahl Pollenschläuche ausbilden. Die Ursache der Pollensterilität wird darin gefunden, dass »evidently not all chromosomes of *P. humile* differently combinated with the chromosomes of *P. sativum* during the formation of gametes, are able to give rise to viable combinations» (l. c. S. 366). In der Nachkommenschaft des F_1-Bastards befanden sich verschiedene Formen mit stark abweichendem Aussehen; die Zytologie dieser Pflanzen war auch normal, trotzdem sie stark steril zu sein schienen.

Ich will jetzt über meine zytologischen Beobachtungen in den von DE HAAN hergestellten Bastarden berichten.

PISUM HUMILE × P. FULVUM.

Von dieser Kreuzung wurden einige Pflanzen untersucht, aber nur von einer konnte die Reduktionsteilung untersucht werden. In der Metaphase der ersten Reifeteilung wurde die Chromosomenpaarung studiert. Es wurde aber nur eine ganz gewöhnliche Paarung beobachtet, nämlich sieben Bivalente (Fig. 1 *a*). Die folgende Anaphase

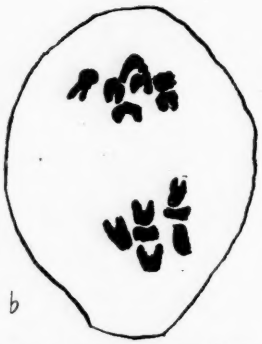


a

war sehr regelmässig (Fig. 1 *b*). Man kann also zwischen der Reduktionsteilung dieses Artbastards und der einer gewöhnlichen Erbse keinen Unterschied feststellen.

PISUM HUMILE × ARVENSE, I.

Es wurden zwei verschiedene Kreuzungen untersucht, die auch eine verschiedene Zytologie zeigten, weshalb sie hier gesondert beschrieben werden. Zuerst wird F_1 d 94.5—1933 behandelt. Es waren halbsterile Pflanzen.



b

Fig. 1. *Pisum humile* × *fulvum*. *a*: Die Chromosomenpaarung in Metaphase I. — *b*: Anaphase I.

Die Reduktionsteilung konnte in verschiedenen Pflanzen studiert werden. Es war immer eine Verkettung von vier Chromosomen in der ersten Metaphase vorhanden. Fig. 2 *d* zeigt die Chromosomenpaarung in einer Pollenmutterzelle. Hier ist ein ringförmiges Amphibivalent vorhanden. Fig. 2 *a* und *b* zeigen die Chromosomenanordnungen in zwei anderen Pollenmutterzellen, in der einen gab es eine Kette, in der anderen einen Ring aus vier Chromosomen. In Fig. 2 *c* sind einige verschiedene Typen von Amphibivalenten abgebildet. Die Chromosomen sind wie ersichtlich bisweilen zickzackorientiert, was zur Bildung von fertilen Pollenkörnern führen muss. Die erste Anaphase verlief trotz der Ringbildung in der Regel ohne Störungen (Fig. 2 *e*).

Wir finden also, dass die Reduktionsteilung in diesem Artbastard in derselben Weise verläuft wie bei einer gewöhnlichen semisterilen Erbse. Ein Amphibivalent ist vorhanden, seine Chromosomen sind oft zickzackorientiert, die Anaphase findet ohne grössere Störungen statt. LUTKOV fand wie erwähnt eine andere Zytologie in *Pisum humile* × *P. sativum*, nämlich sieben Bivalente. *P. arvense* kann wohl nicht als eine von *sativum* verschiedene Art angesehen werden. Die zytologischen Befunde, die hier geschildert wurden, stimmen also kaum mit denen von LUTKOV überein. Es ist aber klar, dass in einem Material wie *Pisum*, wo innerhalb derselben Art verschiedene Chromosomenrassen vorhanden sind, die Artbastardierungen zu ganz verschiede-

nen Ergebnissen führen können, je nach den Rassen die gekreuzt werden.

PISUM HUMILE × P. ARVENSE, II.

Dieser Bastard entstammt einer anderen Kreuzung als Bastard I. Die Kulturnummer war 16 d—1933. Die Zytologie dieses Bastards war von der soeben beschriebenen abweichend. Wahrscheinlich liegt hier

Fig. 2. *Pisum humile* × *arvense*, I. *a*, *b* und *d*: Die Chromosomenpaarung in der Metaphase I, ein Amphibivalent ist vorhanden. — *c*: Amphibivalente aus verschiedenen Pollenmutterzellen. — *e*: Anaphase I.

ein Bastard vor, der ganz normale Chromosomenpaarung hat, der aber in bezug auf eine Inversion in einem der Chromosomen heterozygotisch ist, was die Entstehung verschiedener zytologischer Störungen veranlasst. Ich will zuerst die chromosomalen Befunde schildern.

Die Chromosomenpaarung in der Metaphase I zeigt Fig. 3. Irgend

ein Chromosomenfragment, wie es später so oft zu sehen ist, kann in der Metaphase I nicht beobachtet werden. Die Chromosomenpaarung zeigt in diesem Material eine Variation. Es können in der Pollenmutterzelle sieben Bivalente vorhanden sein, wie Fig. 3 *c* zeigt. Ebenso häufig ist aber eine andere Anordnung, nämlich fünf Bivalente und eine Verkettung von vier Chromosomen. In Fig. 3 *a* ist schliesslich die Anordnung in einer Zelle mit fünf Bivalenten, einem Trivalent und einem Univalent abgebildet.

In der ersten Anaphase sind einige Eigentümlichkeiten zu sehen. Es liegt ein kleines Chromosomenfragment in dem Plasma der Pollenmutterzelle während eine Chromatinbrücke zwei Anaphase-Chromosomen verbindet (Fig. 4 *a* und *b*). In der frühen Telophase ist dieses

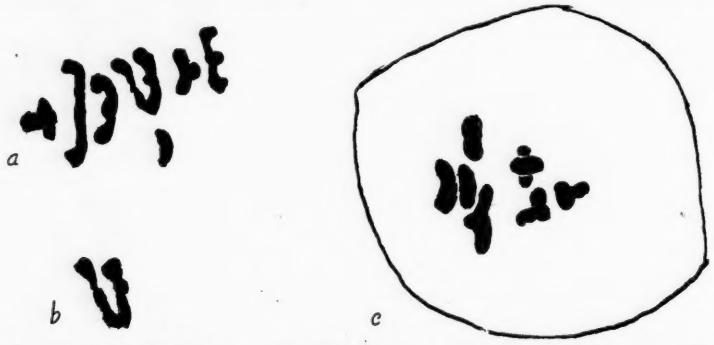


Fig. 3. *Pisum humile* × *arvense*, II. Die Chromosomenpaarung in der ersten Metaphase. *a*: $5_{II} + 1_{I} + 1_{III}$. — *b*: Quadrivalent (oder Amphibivalent). — *c*: 7_{II}.

Chromosomenbild auch zu sehen (Fig. 4 *d*). Bisweilen sah man eine Chromosomenbrücke ohne dass anscheinend ein Fragment vorhanden war. Man kann wohl vermuten, dass das Fragment in der Pollenmutterzelle verborgen war, aber im Schnitt nicht zu unterscheiden war. Einige Male war ein Fragment aber keine Chromosomenbrücke zu sehen (Fig. 4 *c*). In den letztgenannten Zellen war wohl die Chromosomenbrücke zerrissen.

Es wurden einige Zählungen gemacht um die Häufigkeit des Vorkommens des Chromosomenfragments zu bestimmen. In einem Pollenfach wurden 40 Pollenmutterzellen während der ersten Anaphase studiert; in sieben von diesen war ein Fragment und gleichzeitig eine Chromatinbrücke zu sehen. Nicht selten war das Zurückbleiben eines Univalents in der ersten Anaphase festzustellen. In den erwähnten 40 Zellen wurde es sechs Male beobachtet.

In der späten Anaphase wird die Chromatinbrücke zerrissen. Das Chromosomenfragment ist aber während der Interkinese in der Pollenmutterzelle häufig zu sehen. Es liegt in den Pollenmutterzellen zwischen den Interkinesenkernen. In der zweiten Teilung war das Chromosomenfragment auch oft zu sehen. Wie höchst wahrscheinlich ist,

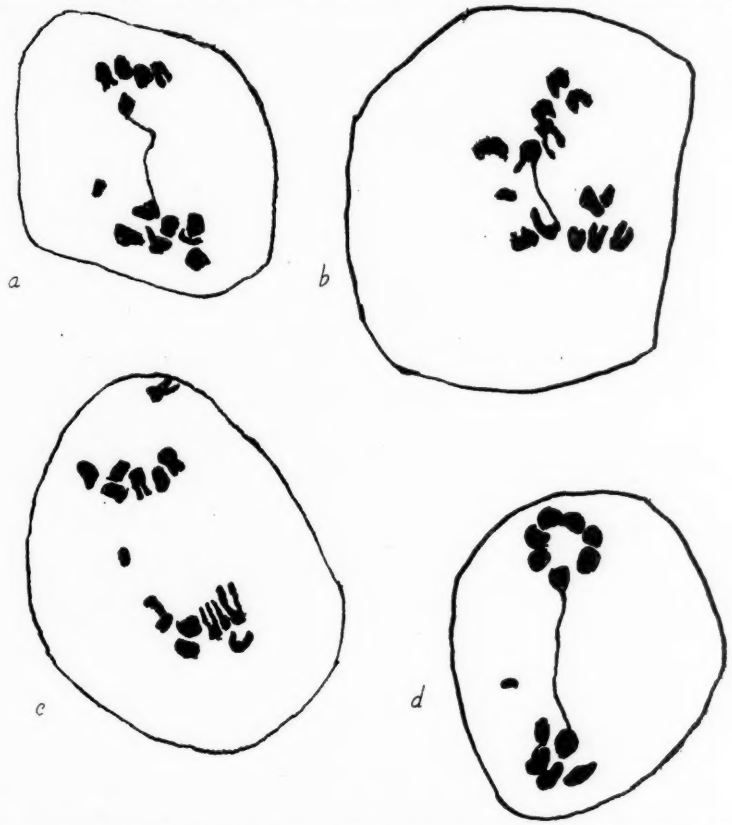


Fig. 4. *Pisum humile* × *arvense*, II. Anaphase I. *a*, *b* und *d*: Chromosomenbrücke und Fragment. — *c*: Nur Fragment.

kommt oft ein langes Chromosom mit zwei Spindelanheftungen vor. Es verhält sich wohl so, dass dieses Chromosom in der ersten Anaphase bisweilen nicht zerrissen wird, was zur Folge hat, dass dieses Chromosom in der zweiten Teilung in verschiedener Weise auf den Polen verteilt wird. In der zweiten Teilung macht sich das Vorkommen von

zwei Spindelanheftungen geltend, und das Chromosom wird in verschiedener Weise auf die beiden Kernteilungsfiguren aufgeteilt (Fig. 5 und 6 *c*).

Die Zytologie dieses *Pisum*-Bastards zeigt die grösste Ähnlichkeit mit der einiger Rassen von *Zea mays*, in denen eine Inversion eines Stückes in einem Chromosom stattgefunden hat (Mc CLINTOCK, 1933,

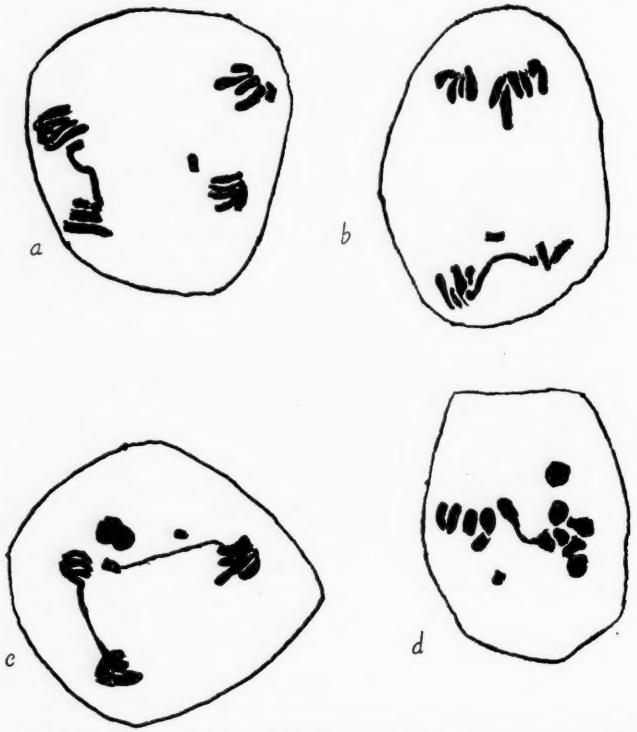


Fig. 5. *Pisum humile* × *arvense*, II. *a* und *b*: Anaphase II, Chromosomenbrücke und Fragment, *c*: Zwei Brücken und Fragment, *d*: Metaphase II, Chromosomenbrücke und Fragment.

S. 203). In der letztgenannten Abhandlung wurde auch die Prophase der Reduktionsteilung untersucht, was in *Pisum* kaum geschehen kann. Die Übereinstimmung mit dieser Untersuchung ist aber betreffs der ersten Anaphase sehr gross. In den Mais-Kreuzungen war oft eine Brücke zwischen zwei Chromosomen und ein Fragment zu beobachten. Diese Chromosomenkonfiguration wurde aber sehr plausibel erklärt.

In einem der Chromosomen hat eine Inversion eines Chromosomenfragments stattgefunden. Der fragliche Typus ist betreffs dieser Inversion heterozygotisch. Erfolgt dann ein Crossing-over zwischen dem invertierten Segment und dem unveränderten Segment in der Prophase der ersten Reifeteilung und geschieht, wie von Mc CLINTOCK ausgeführt wurde und wie gezeigt worden ist, der Austausch zwischen zwei Chromatiden, so entsteht ein Chromatid mit zwei Anfestungspunkten für Spindelfasern, ausserdem aber ein Chromosomenfragment ohne Anheftungen, das dadurch ausserhalb des Chromosomengeschehens gelangt.

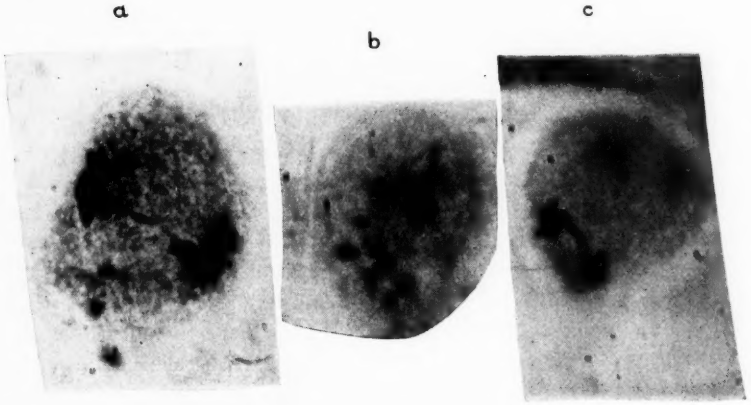


Fig. 6. *a* und *b*: Die erste Anaphase der Reifeteilung. Ein Fragment und ein Chromosom mit zwei Anheftungen sind vorhanden. — *c*: Die Telophase der zweiten Reifeteilung. Fragment und Chromosom mit zwei Anheftungen. — (Photo: O. MATTSSON.)

Es ist also anzunehmen, dass in diesem *Pisum*-Bastard eine Chromosomeninversion vorhanden ist, im übrigen erscheint aber die Chromosomenpaarung ganz normal, wie bei einer gewöhnlichen *Pisum*-Pflanze.

Es sind aber einige andere Beispiele für Chromosomenfragmentation beschrieben, die für eine ähnliche Verteilung der Teile in dem Chromosom sprechen. In einem Artbastard, *Crepis divaricata* × *dicoccoides*, ist in der ersten Metaphase eine sehr variierende Paarung konstatiert. Oft wurden Brücken zwischen den Anaphasechromosomen und Fragmente beobachtet (MÜNTZING, 1934).

Es können schliesslich einige Beispiele aus der neueren Literatur erwähnt werden, die in ähnlicher Weise gedeutet wurden. So der Fall

von SMITH bei *Trillium erectum* (SMITH, 1935) und der von MATHER bei einem triploiden Weizenbastard (MATHER, 1935).

SUMMARY.

In the species cross *Pisum humile* × *fulvum* there are seven bivalents in the first metaphase.

In the cross *Pisum humile* × *arvense*, I there are five bivalents and an amphibivalent in the first metaphase of the meiosis.

In the cross *Pisum humile* × *arvense*, II there are seven bivalents or five bivalents and an amphibivalent in the first metaphase. In the first anaphase a chromosome fragment and a chromosome bridge were often observed between two chromosomes. This indicates an inversion in one of the chromosomes.

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DIE ZYTOLOGIE EINES TRISOMISCHEN PISUM-TYPUS

VON *ARTUR HÅKANSSON*
LUND

IN einer Abhandlung in diesem Band von Hereditas hat ERNST NILSSON einen eigentümlichen Erbsentypus beschrieben, der *Pisum elatius* ähnlich ist (siehe S. 179). Dieser Typus kommt regelmässig in den Nachkommen des Semisterilitätsfalles N4 oder in Kreuzungen zwischen N4 und anderen Serien vor. Mit N4 werden semisterile Pflanzen bezeichnet, die Kreuzungsprodukte zwischen der Sorte Extra Rapid und anderen Linien sind. Der *elatius*-Typus ist ausser durch den eigentümlichen Phänotypus durch schwache Vitalität ausgezeichnet.

Von diesem *elatius*-Typus habe ich in den Sommern 1934 und 1935 zahlreiche Blütenknospen fixiert. Er erwies sich als trisomisch. In mehreren Pflanzen wurde die somatische Chromosomenzahl im sterilen Gewebe der Anthere oder in den Wandzellen des jungen Fruchtknotens bestimmt. Immer wurden 15 Chromosomen gezählt (Fig. 1).

Nach Feststellen der Chromosomenzahl war ich bestrebt die Chromosomenpaarung in der Metaphase in den Pollenmutterzellen zu studieren. Ein sehr grosses Material wurde geschnitten, es wurde aber nur ein einziges Präparat mit Reduktionsteilungen erhalten. Man kann also nicht sicher sein, dass alle Konjugationsverhältnisse der Chromosomen, die in diesem Typus möglich sind, in dem untersuchten Material realisiert wurden.

Die Ergebnisse der Studien über die Chromosomenpaarung sind folgende. In der ersten Metaphase wurden oft ein Trivalent und sechs Bivalente beobachtet. Das Trivalent hatte wie erwartet ein sehr verschiedenes Aussehen. Am häufigsten ist ein V-förmiges Trivalent (Fig. 2 *c*). Die Anaphase einer mit dieser Chromosomenanordnung ausgerüsteten Zelle zeigt Fig. 2 *d*. Ein anderes Trivalent ist in Fig. 2 *f* abgebildet. Die drei Chromosomen sind hier in einer Reihe angeordnet. Chiasmata sind zwischen den Chromosomen ausgebildet. Schliesslich ist eine neue Trivalentform in Fig. 2 *b* abgebildet, »ring-and-rod» ist eine gebräuchliche Bezeichnung eines solchen Trivalents.

Nicht immer ist ein Trivalent in den Pollenmutterzellen vorhanden. Eine gewöhnliche Chromosomenpaarung ist sieben Bivalente und ein

Univalent. Das Trivalent ist also in ein Bivalent und ein Univalent zerfallen. Die dadurch entstandene Chromosomenanordnung scheint

Fig. 1. Somatische Kernplatten.

beinahe ebenso häufig zu sein wie sechs Paare und ein Trivalent. Man kann schliesslich noch eine Chromosomenanordnung konstatieren, die

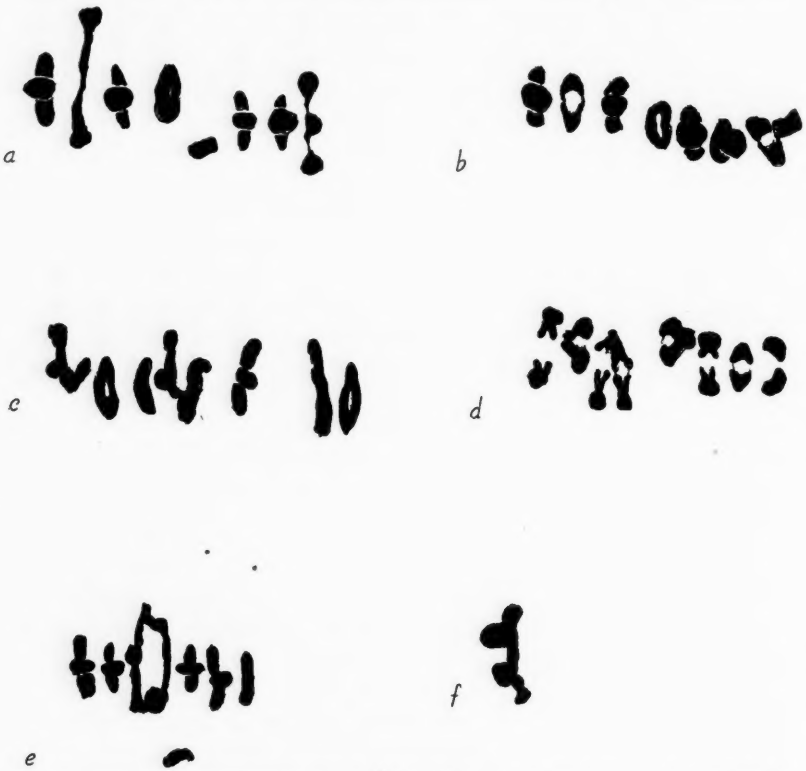

Fig. 2. Die Chromosomenpaarung in Metaphase I. *a*: $7_{II} + 1_{I}$. — *b*, *c* und *d*: $6_{II} + 1_{III}$. — *e*: $5_{II} + 1_{I} + 1_{IV}$ (?). — *f*: Trivalent.

einige Male beobachtet wurde. Ein Amphibivalent ist bisweilen zu beobachten, ein Ring aus vier Chromosomen ist in Fig. 2 *e* abgebildet.

Die erste Anaphase der Reifeteilung geschah oft in der Weise, dass acht Chromosomen nach dem einen Pole, sieben nach dem andern wanderten (Fig. 3 *d*). Wenn aber ein Univalent in einem früheren Stadium in der Zelle vorhanden war, sieht die Anaphase anders aus. Das Univalent wird nämlich in der Regel längsgespaltet. Fig. 3 *a* zeigt, dass die Teilung des Univalents so spät geschah, dass die Spalthälften nicht in die Interkinesenkerne einverleibt wurden. Es wurde oft beobachtet, dass das Univalent während der Teilung nahe dem einen Pole lag. Trotzdem wurde es aber längsgeteilt und die beiden Spalthälften gingen nach verschiedenen Polen (Fig. 3 *b* und 3 *c*).

Trisomische Pflanzen sind schon früher in *Pisum* gefunden worden, nämlich von SANSOME (SANSOME, 1933). Zwei solche fanden sich in den

Fig. 3. *a*, *b* und *c*: Anaphase I mit Längsspaltung des Univalents. — *d*: Anaphase I mit der Chromosomenverteilung 8 + 7.

Nachkommen des Bastarden zwischen der K-Linie und der Thibet-Linie. Dieser Bastard zeichnet sich zytologisch durch einen 6-Ring aus.

Der in dieser Abhandlung geschilderte *elatius*-Typus kommt, wie NILSSON konstatierte, regelmässig in der Nachkommenschaft von N4 oder in Kreuzungen mit N4 vor. N4 hat einen Ring aus vier Chromosomen (HÅKANSSON, 1934). Es erscheint am wahrscheinlichsten, dass eine Nichttrennung unter den Ringchromosomen die Bildung eines recht hohen Prozents von Gonen mit einem überzähligen Chromosom veranlasst. Die Zahl der trisomischen Pflanzen ist nämlich ziemlich gross, so in einem Versuch 20 *elatius* : 189 Normalpflanzen (NILSSON l. c.). Nichttrennung ist in Pflanzen mit Chromosomenverkettung häufig, nur in N4 scheinen aber vitale Gonen mit acht Chromosomen zu entstehen; hier sind ja auch teilweise andere Chromosomen verändert als in den anderen Semisterilitätsfällen (HÅKANSSON l. c.). Gegen die Annahme,

dass der *elatius*-Typus infolge Nichttrennung unter den Ringchromosomen in N4 entsteht spricht allerdings, dass ich keine Verkettung von fünf Chromosomen in *elatius* beobachten konnte. Wie aber erwähnt wurde, ist das untersuchte Material klein, weshalb die in Frage stehende Konfiguration vielleicht nur zufällig nicht gefunden worden ist.

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THE F_3-TEST OF HOMOMERIC F_2-SEGREGATIONS

BY *GERT BONNIER* AND *OLOF TEDIN*
WIAD AND SVALÖF

1.

AS is well known, characters governed by homomeric factors segregate in F_2 in one of the following ratios:

3	dominant	: 1	recessive	(monomeric)
15	»	: 1	»	(dimeric)
63	»	: 1	»	(trimeric)
255	»	: 1	»	(tetrameric), etcetera.

When the number of individuals in F_2 is small, it is often impossible to determine the number of factors with any degree of certainty. It is, therefore, necessary to grow the F_3 progeny from each dominant F_2 plant, in order to classify the latter into homozygotes and different types of heterozygotes. It is an elementary fact that F_2 plants, giving F_3 progenies segregating in different ratios, are expected to occur in the proportions given in Table 1.

TABLE 1. *Expected proportions of F_2 plants, giving F_3:s segregating in different ratios.*

	Constant dominants	Segregation in F_3 in the ratio			
		3 : 1	15 : 1	63 : 1	255 : 1
monomeric...	1	2	—	—	—
dimeric	7	4	4	—	—
trimeric	37	6	12	8	—
tetrameric ...	175	8	24	32	16

When the number of individuals in the separate F_3 families is small it is again often impossible to ascertain to which segregation-class the F_2 plants really belong. Tri- and tetraheterozygous F_2 plants, especially, will often, with a limited number of individuals in F_3, give no visible

segregation and thus be classified in a wrong group. It may, therefore, be necessary to make a close analysis of the material in order to ascertain the true number of homomeric factors involved. BERNSTEIN and FAUST (1922) have offered one solution of the problem. In this paper an alternative solution will be given, an attempt being also made to arrive at an approximative solution in cases, where the number of individuals is different in different F_3 families.

2.

The problem presents theoretical difficulties only when the progenies of the different F_2 plants have different numbers of individuals, and in this case there does not seem to exist an exact solution. On the other hand, it is only rarely possible to obtain the same number of individuals in each F_3 family; in most cases these numbers will, on the contrary, vary within wide limits. A solution that does not account for this difficulty will therefore be of mainly academical interest, and rarely applicable to actual experimental material. In order to reach an approximate solution for varying numbers in F_3 it is necessary, however, at first to elaborate a method under the assumption that all F_3 families have an equal number of individuals — say n. In section 4 a tentative solution of the more complex problem will be offered.

Suppose that we have N F_2 plants, all phenotypically alike but genetically belonging to h different groups, consisting of $\alpha_1, \alpha_2, \ldots . \alpha_h$ plants respectively. Thus:

$$\alpha_1 + \alpha_2 + \ldots\ldots\ldots + \alpha_h = N \tag{1}$$

The numbers α are unknown and must be estimated by the aid of the results in F_3. All F_2 plants belonging to one and the same group will segregate in the same ratio in F_3 with variations due to random sampling. Let therefore p be the probability that an F_3 plant in the progeny of an F_2 plant belonging to the group numbered i, will be a recessive, and q_i the corresponding probability that such an F_3 plant will be a dominant. Hence $p_i + q_i = 1$. In the different groups the values of p and q will be:

constant dominants : $p = 0,\ q = 1$
segregation in 3 : 1 : $p = 1/4,\ q = 3/4$
» » 15 : 1 : $p = 1/16,\ q = 15/16$
» » 63 : 1 : $p = 1/64,\ q = 63/64$
» » 255 : 1 : $p = 1/256,\ q = 255/256$

By developing the binomial $(p_i + q_i)^n$ and multiplying this with α_i (the number of F_2 plants in group i) we find the numbers of F_2 plants of this group, which will give rise to 0, 1, 2 . . . r recessives in F_3. The binomial coefficients of the order n are as usually denoted

$$1, \binom{n}{1}, \binom{n}{2}, \binom{n}{3} \ldots\ldots\ldots\ldots$$

There will be:

$\alpha_i q_i^n$	plants in this group which in F_3 give rise to	0 recessives
$\alpha_i p_i q_i^{n-1}\binom{n}{1}$	» » » » » » » » » »	1 »
$\alpha_i p_i^2 q_i^{n-2}\binom{n}{2}$	» » » » » » » » » »	2 »
— —		
$\alpha_i p_i^r q_i^{n-r}\binom{n}{r}$	» » » » » » » » » »	r »

For each of the h groups of F_2 plants it is now possible, in the same manner, to determine the number of plants that in F_3 will give rise to 0, 1, 2 . . . r recessives. For the sake of simplicity we write:

$$p_i^r q_i^{n-r}\binom{n}{r} = x_{ir} \tag{2}$$

Denote by y_r the actually observed number of F_2 plants, which in F_3 have given rise to r recessives. This number must evidently be equal to the sum of the x values for all h groups. Then for each of the $n+1$ values, that r may assume ($r = 0, 1, 2 \ldots n$) we obtain an equation of the following kind (in which the suffix r has been omitted):

$$\alpha_1 x_1 + \alpha_2 x_2 + \ldots\ldots\ldots + \alpha_h x_h = y \tag{3}$$

In these equations the α:s are unknown, all the other values are either computable (the x:s) or observed in the experiment (the y:s). The best solutions of these equations, in regard to the α:s, will give the best estimate available of the number of F_2 plants in the different segregation-classes. These estimates of the values α are denoted $a_1, a_2 \ldots a_h$. The best solution of the $n+1$ equations (3) is to be found by the method of the least square. Thus the values a are obtained by solving the h equations.

$$(4) \qquad \begin{aligned} a_1 S(x_1-\bar{x}_1)^2 + a_2 S[(x_1-\bar{x}_1)(x_2-\bar{x}_2)] + \ldots\ldots\ldots = \\ = S[(x_1-\bar{x}_1)(y-\bar{y})] \\ a_1 S[(x_1-\bar{x}_1)(x_2-\bar{x}_2)] + a_2 S(x_2-\bar{x}_2)^2 + \ldots\ldots\ldots = \\ = S[(x_2-\bar{x}_2)(y-\bar{y})] \end{aligned}$$

etc., i. e. the solution is identical with the calculation of partial regression coefficients.

The computation of the values x may be checked by the relations:

$$(5) \qquad S(x_1) = S(x_2) = \ldots\ldots\ldots = S(x_h) = 1$$

In conformity to the relation (1) we should expect that

$$(6) \qquad a_1 + a_2 + \ldots\ldots\ldots + a_h = N,$$

but the quantities a are solutions of the equations (4) and therefore do not exactly satisfy the equations (3). Consequently, we cannot expect them to satisfy exactly the relation (6). In the χ^2-test, to be discussed later, we must, therefore, make a proportional reduction of the estimates a, so that their sum will equal N.

3.

The most likely number of acting homomeric factors is determined by the following procedure:

The residual variance, s^2, is defined by the equation

$$(7) \qquad s^2 = \frac{S(a_1x_1 + a_2x_2 + \ldots\ldots\ldots + a_hx_h - y)^2}{n-h}$$

That is to say: for each possible hypothesis (i. e. for each possible value of h, for dimeric, trimeric, tetrameric etc. factors) we compute, by the aid of the values a and x, the numbers of F_2 plants expected to give 0, 1, 2 etc. recessives. Then the differences between these expected numbers and those actually found are determined and squared, and these squares for all possible numbers of recessives are added, the sum then being divided by $n-h$. The values x are the terms of the binomial, as defined in (2), and the values a to be used are the theoretical ones, which are obtained by the aid of Table 1. For the three most common hypotheses these values are:

dimeric factors: $a_1 = 7N/15,\ a_2 = 4N/15,\ a_3 = 4N/15$
trimeric » : $a_1 = 17N/63,\ a_2 = 6N/63,\ a_3 = 12N/63,\ a_4 = 8N/63$
tetrameric » : $a_1 = 175N/255,\ a_2 = 8N/255,\ a_3 = 24N/255,$
$a_4 = 32N/255,\ a_5 = 16N/255.$

The hypothesis which gives the smallest value of s^2 is then of the greatest likelihood.

It should be observed that the determination of the most likely number of homomeric factors can be made without the computation of the estimates a of the expected values α. But if we want to test whether there is a good agreement between the most likely hypothesis and the data found, the more elaborate method must be used. Disturbances in the Mendelian ratios, caused by differences in vitality or other factors, can thus be detected only by calculating the a values and applying the χ^2-test, to be discussed later.

4.

When there is a different number of individuals in different F_3 families it is impossible to deduce directly the most probable number of families giving rise to a certain number of recessives. In such cases, therefore, a less exact method must be used, for example the following:

The existing different values of n are classified in groups, say t, so chosen that their central values will be integers. If we then make the assumption that in each of the above-mentioned h groups of F_2 plants the (unknown) distribution of n:s is the same as in the whole material, it is possible to solve the problem. It must be remembered that this assumption is rarely quite exact, and anyway the distributions of n:s in the different groups must vary within the limits of random sampling. If, on the other hand, these distributions are essentially different in the h groups, these differences must have an actual biological cause. If they cause a significant discrepancy between the values a, computed by the following method, and the theoretical α values of a given (the most likely) hypothesis, this discrepancy is biologically significant and its occurrence, consequently, valuable.

If the found frequency distribution of the n:s in the material as a whole is distinctly irregular, it may be advisable to smooth this distribution. Denote the central values of the t groups by

$$n_1,\ n_2 \ldots\ldots n_v \ldots\ldots n_t$$

and let the smoothed relative numbers of F_3 families in the different groups be

$$f_1,\ f_2 \ldots\ldots f_v \ldots\ldots f_t$$

(where thus $f_1 + f_2 + \ldots\ldots + f_t = 1$).

We may then expect that of the $\alpha_i F_2$ plants belonging to the group numbered i there will be $f_v \alpha_i$ which get a progeny of approximately n_v individuals. By the same deduction as before, we may therefore expect that of these $f_v \alpha_i F_2$ plants

$$f_v \alpha_i p_i^r q_i^{n_v - r} \binom{n_v}{r}$$

will give rise to r recessives in F_3.

The solution of the problem is then given by the same method as in section 2, if, instead of the definition of x_{ir} given there, we only use the following definition

$$(8) \qquad x_{ir} = f_1 p_i^r q_i^{n_1 - r} \binom{n_1}{r} + f_2 p_i^r q_i^{n_2 - r} \binom{n_2}{r} + \ldots + f_t p_i^r q_i^{n_t - r} \binom{n_t}{r}$$

When comparing the residual variances s^2 we have to substitute the number n_t for the number n of the formula in section 3.

5.

As an example a case described by NILSSON-EHLE (1914) will be used here. He crossed a red and a white wheat and in F_2 he got 58 plants, all of which were red. Thus $N = 58$. The results in F_3 are shown in Table 2.

From this NILSSON-EHLE concludes that the cross is a trimeric one.

Taking together all families with the same number of recessives we get Table 3.

We have grouped the different values n in 8 groups with a grouping-unit of 7 and the central values

$n_1 = 22$, $n_2 = 29$, $n_3 = 36$, $n_4 = 43$, $n_5 = 50$, $n_6 = 57$, $n_7 = 64$, $n_8 = 71$.

(The highest value of n, 75, is taken to belong to the highest group.) The frequency-distribution of F_3-families in the different n-groups is therefore:

3, 4, 6, 9, 11, 9, 7, 9,

which distribution was smoothed to be:

3, 4, 6, 9, 11, 9, 8, 8.

Hence

$$f_1 = \frac{3}{58}, f_2 = \frac{4}{58}, f_3 = \frac{6}{58}, f_4 = \frac{9}{58}, f_5 = \frac{11}{58}, f_6 = \frac{9}{58}, f_7 = \frac{8}{58}, f_8 = \frac{8}{58}.$$

TABLE 2.

Total number in F_3 (n)	Number of recessives in F_3	Total number in F_3 (n)	Number of recessives in F_3
21	0	52	0
25	0	52	1
25	0	52	3
26	0	53	2
28	0	54	1
29	1	54	4
32	0	55	6
33	0	55	12
34	0	57	3
34	0	57	3
37	0	57	5
38	2	57	17
38	4	60	0
41	0	61	14
41	0	63	0
42	0	63	0
44	0	64	0
44	3	65	0
45	7	65	4
46	0	67	0
46	0	68	0
46	0	68	0
47	0	68	1
47	1	69	0
48	0	69	4
49	0	71	0
49	3	72	0
51	0	74	0
52	0	75	0

The computations are very laborious and if the method is to be more generally applicable it is necessary to have tables giving the values of

$$p^r q^{n-r}\binom{n}{r}$$

We have computed tables of these values for

$n = 22, 29, 36, 43, 50, 57, 64, 71$ [1] and for the following values of p

[1] Tables of the terms of the binomial (with 5 decimals) have been computed by BERNSTEIN and FAUST (1922) for $n = 49$ and $p = \frac{1}{4}, \frac{1}{16}, \frac{1}{64}$.

$p_1 = 0$, $p_2 = \frac{1}{4}$, $p_3 = \frac{1}{16}$, $p_4 = \frac{1}{64}$, $p_5 = \frac{1}{256}$ (See Table 6).

Using these tables the values of the different x:s (formula 8) have been calculated (Table 4). This table should include all values of the x:s from $r = 0$ to $r = 71$ (i. e. to $r = n_t$), but the x:s are calculated only to $r = 40$, since from $r = 40$ all x:s are less than 0,000000001.

TABLE 3.

Number of families	Number of recessives
36	0
5	1
2	2
5	3
4	4
1	5
1	6
1	7
1	12
1	14
1	17

If we now take the hypotheses dimeric, trimeric and tetrameric factors (i. e. $h = 3, 4, 5$) as the possible ones, we must for each of these hypotheses compute the corresponding residual variances s^2. The computations give:

hypothesis dimeric factors:

$$s^2 = \frac{S\left(\frac{7}{15} \cdot 58x_1 + \frac{4}{15} \cdot 58x_2 + \frac{4}{15} \cdot 58x_3 - y\right)^2}{71 - 3} = 1{,}32066;$$

hypothesis trimeric factors:

$$s^2 = \frac{S\left(\frac{37}{63} \cdot 58x_1 + \frac{6}{63} \cdot 58x_2 + \frac{12}{63} \cdot 58x_3 + \frac{8}{63} \cdot 58x_4 - y\right)^2}{71 - 4} = 0{,}294001;$$

hypothesis tetrameric factors:

$$s^2 = \frac{S\left(\frac{175}{255} \cdot 58x_1 + \frac{8}{255} \cdot 58x_2 + \frac{24}{255} \cdot 58x_3 + \frac{32}{255} \cdot 58x_4 + \frac{16}{255} \cdot 58x_5 - y\right)^2}{71 - 5} = 2{,}067970.$$

TABLE 4.

r	x_1	x_2	x_3	x_4	x_5	y
0	1	0,000112754	0,057994711	0,462739906	0,821937212	36
1		0,000886293	0,147020877	0,347879871	0,160255856	5
2		0,003422247	0,203403336	0,139711679	0,016550624	2
3		0,008748524	0,202953425	0,039288798	0,001187543	5
4		0,016917302	0,161884129	0,008578676	0,000065739	4
5		0,026925092	0,108451792	0,001534267	0,000002966	1
6		0,037538883	0,062757530	0,000232174	0,000000113	1
7		0,047996930	0,031939262	0,000030411	0,000000004	1
8		0,057937870	0,014477478	0,000003493		
9		0,066958033	0,005899712	0,000000357		
10		0,074396792	0,002177054	0,000000033		
11		0,079495741	0,000731675	0,000000003		
12		0,081684767	0,000225038			1
13		0,080755524	0,000063598			
14		0,076877821	0,000016574			1
15		0,070515436	0,000003995			
16		0,062316350	0,000000893			
17		0,053014877	0,000000186			1
18		0,043353837	0,000000036			
19		0,034014516	0,000000006			
20		0,025551512	0,000000001			
21		0,018341197				
22		0,012558295				
23		0,008190596				
24		0,005082252				
25		0,002997628				
26		0,001679631				
27		0,000893502				
28		0,000451159				
29		0,000216169				
30		0,000098264				
31		0,000042370				
32		0,000017327				
33		0,000006719				
34		0,000002470				
35		0,000000861				
36		0,000000284				
37		0,000000089				
38		0,000000026				
39		0,000000007				
40		0,000000002				
Total:	1	0,999999949	1,000001308	0,999999668	1,000000057	58

In accordance with NILSSON-EHLE's solution we thus find that the hypothesis trimeric factors is the likeliest.

When this is stated we may proceed to the determination of the quantities a. In order to determine these quantities we construct the equations (4) for the hypothesis trimeric factors, and obtain

$$\begin{aligned}
0{,}9861111\ a_1 - 0{,}0137761\ a_2 + 0{,}0441058\ a_3 + 0{,}4488510\ a_4 &= 35{,}1944444\\
-0{,}0137761\ a_1 + 0{,}0456785\ a_2 - 0{,}0002538\ a_3 - 0{,}0125097\ a_4 &= -0{,}3547703\\
0{,}0441058\ a_1 - 0{,}0002538\ a_2 + 0{,}1368293\ a_3 + 0{,}1020555\ a_4 &= 4{,}2898591\\
0{,}4488510\ a_1 - 0{,}0125097\ a_2 + 0{,}1020555\ a_3 + 0{,}3423987\ a_4 &= 18{,}1044593
\end{aligned}$$

of which the solutions are

$$a_1 = 32{,}616957,\ a_2 = 3{,}584406,\ a_3 = 16{,}976344,\ a_4 = 5{,}178842.$$

The sum of these estimates is, however, not exactly 58 but $58{,}356549$. Thus, if we wish to make a χ^2-test we have first to multiply the estimates by

$$\frac{58}{58{,}356549} = 0{,}993890$$

whereby we find the corrected estimates to be

$$a_1' = 32{,}417667,\ a_2' = 3{,}562505,\ a_3' = 16{,}872619,\ a_4' = 5{,}147199.$$

The χ^2-test is found in Table 5.

TABLE 5.

	a_1	a_2	a_3	a_4	Total
Theoretically expected on 58	34,063492	5,523810	11,047619	7,365079	58,000000
Corrected estimates	32,417667	3,562505	16,872619	5,147199	57,999990
$\frac{\text{Difference}^2}{\text{expected}}$	0,079520	0,696388	3,071307	0,667880	4,515095

We have here 3 degrees of freedom. (The fact that we here do not compare *expected* with *found* frequencies, but do compare *expected* with *estimated* frequencies has no influence upon the number of degrees of freedom. What we are in reality asking is whether 4 — in some way or other calculated — frequencies may, or may not, within the limits of random sampling, coincide with 4 expected frequencies.)

From tables of χ^2 [for instance the table in FISHER (1934, Chapter IV)] we find that the value $\chi^2 = 4{,}515095$ and 3 degrees of freedom means

TABLE 6. *Tables of* $\binom{n}{r}p^r q^{n-r}$ *or* $\frac{n!}{r!\,(n-r)!}p^r q^{n-r}$

$$p=\frac{1}{4} \qquad q=\frac{3}{4}$$

r	$n=22$	$n=29$	$n=36$	$n=43$	$n=50$	$n=57$	$n=64$	$n=71$
0	0,001783806	0,000238110	0,000031784	0,000004243	0,000000566	0,000000076	0,000000010	0,000000001
1	0,013081223	0,002301725	0,000381405	0,000060811	0,000009439	0,000001436	0,000000215	0,000000032
2	0,045784221	0,010741964	0,002224864	0,000425666	0,000077083	0,000013405	0,000002260	0,000000372
3	0,101742600	0,032224209	0,008405035	0,001939191	0,000411108	0,000081922	0,000015570	0,000002851
4	0,161092148	0,069818951	0,023113867	0,006463981	0,001610171	0,000368651	0,000079153	0,000016157
5	0,193310446	0,116364933	0,049309579	0,016806332	0,004937860	0,001302567	0,000316611	0,000072169
6	0,182570630	0,155153214	0,084922059	0,035480091	0,012344653	0,003762970	0,001037783	0,000264620
7	0,139113782	0,169929883	0,121317207	0,062512529	0,025864982	0,009138635	0,002866256	0,000819062
8	0,086938129	0,155769208	0,146591655	0,093768674	0,046341426	0,019038825	0,006807353	0,002184165
9	0,045078990	0,121153621	0,152020877	0,121552011	0,072086650	0,034551952	0,014116162	0,005096389
10	0,019534206	0,080769130	0,136818959	0,137758984	0,098518523	0,055283101	0,025884780	0,010532540
11	0,007103336	0,046503430	0,107796625	0,137759016	0,119416346	0,078736618	0,042356893	0,019469229
12	0,002170460	0,023251700	0,074858759	0,122452451	0,129367612	0,100607819	0,062358757	0,032448694
13	0,000566528	0,010135380	0,046066979	0,097333932	0,126050465	0,116086016	0,083145019	0,049089080
14	0,000119256	0,003861088	0,025227151	0,069524242	0,111044501	0,121613725	0,100962565	0,067789609
15	0,000021120	0,001287028	0,012333273	0,044804515	0,088835510	0,116208824	0,112179690	0,085867000
16	0,000003092	0,000375375	0,005395806	0,026135958	0,064775940	0,101682670	0,114516921	0,100178041
17	0,000000364	0,000095686	0,002116001	0,013836697	0,043183960	0,081744868	0,107780496	0,108035174
18	0,000000033	0,000021263	0,000744519	0,006662010	0,026390236	0,060551806	0,093809022	0,108035149
19	0,000000002	0,000004103	0,000235111	0,002921979	0,014815560	0,041430162	0,075705526	0,100453773
20		0,000000684	0,000066615	0,001168790	0,007654707	0,026239097	0,056779184	0,087059880
21		0,000000098	0,000016912	0,000426701	0,003645093	0,015410260	0,039655264	0,070477097
22		0,000000012	0,000003845	0,000142245	0,001601633	0,008405604	0,025836000	0,053390173
23		0,000000001	0,000000780	0,000043288	0,000649979	0,004263714	0,015726254	0,037915886
24			0,000000141	0,000012025	0,000243727	0,002013415	0,008955227	0,025277250
25			0,000000023	0,000003046	0,000084492	0,000885904	0,004776127	0,015840412
26			0,000000003	0,000000703	0,000027080	0,000363448	0,002388637	0,009341779
27				0,000000147	0,000008024	0,000139097	0,001120325	0,005189881
28				0,000000028	0,000002197	0,000049678	0,000493453	0,002718510
29				0,000000005	0,000000555	0,000016559	0,000204197	0,001343631
30					0,000000130	0,000005152	0,000079410	0,000627027
31					0,000000028	0,000001496	0,000029031	0,000276431
32					0,000000006	0,000000405	0,000009980	0,000115180
33					0,000000001	0,000000102	0,000003226	0,000045374
34						0,000000024	0,000000980	0,000016904
35						0,000000005	0,000000280	0,000005957
36							0,000000075	0,000001985
37							0,000000018	0,000000626
38								0,000000187
39								0,000000053
40								0,000000014
41								0,000000003

$$p = \frac{1}{16} \qquad q = \frac{15}{16}$$

r	$n = 22$	$n = 29$	$n = 36$	$n = 43$	$n = 50$	$n = 57$	$n = 64$	$n = 71$
0	0,241751005	0,153874664	0,097941432	0,062339757	0,039679300	0,025255942	0,016075415	0,010232009
1	0,354568049	0,297491096	0,235059189	0,178707202	0,132264438	0,095972587	0,068588437	0,048431600
2	0,248198286	0,277659809	0,274235975	0,250190462	0,216031741	0,179148595	0,144035828	0,113007039
3	0,110310142	0,166596283	0,207200287	0,227951204	0,230434127	0,218959495	0,198449041	0,173277171
4	0,034931855	0,072191885	0,113960210	0,151967343	0,180506722	0,197063484	0,201756790	0,196381176
5	0,008383679	0,024064017	0,048623034	0,079023073	0,110710638	0,139258301	0,161405204	0,175433563
6	0,001583587	0,006417090	0,016747931	0,033365300	0,055355346	0,080460315	0,105810097	0,128651243
7	0,000241309	0,001405653	0,004785122	0,011757303	0,023196529	0,039080678	0,058447480	0,079642054
8	0,000030164	0,000257704	0,001156405	0,003527191	0,008312081	0,016283644	0,027762599	0,042475349
9	0,000003128	0,000040087	0,000239847	0,000914456	0,002585982	0,005910361	0,011516342	0,019821822
10	0,000000271	0,000005345	0,000043172	0,000207277	0,000706835	0,001891313	0,004222655	0,008193024
11	0,000000020	0,000000615	0,000006803	0,000041455	0,000171354	0,000538738	0,001381959	0,003028938
12	0,000000001	0,000000062	0,000000945	0,000007370	0,000037127	0,000137677	0,000406910	0,001009646
13		0,000000005	0,000000116	0,000001172	0,000007235	0,000031771	0,000108501	0,000305483
14			0,000000013	0,000000167	0,000001275	0,000006657	0,000026352	0,000084371
15			0,000000001	0,000000022	0,000000204	0,000001272	0,000005856	0,000021374
16				0,000000003	0,000000030	0,000000222	0,000001195	0,000004987
17					0,000000004	0,000000036	0,000000225	0,000001076
18						0,000000005	0,000000039	0,000000215
19							0,000000007	0,000000040
20								0,000000007
21								0,000000001

$$p = \frac{1}{64} \qquad q = \frac{63}{64}$$

r	$n = 22$	$n = 29$	$n = 36$	$n = 43$	$n = 50$	$n = 57$	$n = 64$	$n = 71$
0	0,707184754	0,633369130-	0,567258052	0,508047882	0,455017115	0,407523396	0,364986387	0,326889323
1	0,246953295	0,291550403	0,324147463	0,346762960	0,361125785	0,368711949	0,370779656	0,368398898
2	0,041158820	0,064789030	0,090041041	0,115587606	0,140437767	0,163871887	0,185389872	0,204666085
3	0,004355436	0,009255585	0,016197839	0,025074557	0,035666721	0,047687615	0,060815775	0,074719362
4	0,000328386	0,000954941	0,002121145	0,003980009	0,006652129	0,010218767	0,014721268	0,020162358
5	0,000018762	0,000075789	0,000215482	0,000492773	0,000971422	0,001710345	0,002804052	0,004288505
6	0,000000844	0,000004812	0,000017671	0,000049538	0,000115645	0,000236524	0,000437669	0,000748786
7	0,000000031	0,000000251	0,000001202	0,000004156	0,000011538	0,000027353	0,000057762	0,000110365
8		0,000000011	0,000000069	0,000000297	0,000000984	0,000002714	0,000006510	0,000014014
9			0,000000003	0,000000018	0,000000073	0,000000234	0,000000643	0,000001557
10				0,000000001	0,000000005	0,000000018	0,000000056	0,000000153
11						0,000000001	0,000000004	0,000000013
12								0,000000001

$$p = \frac{1}{256} \qquad q = \frac{255}{256}$$

r	$n = 22$	$n = 29$	$n = 36$	$n = 43$	$n = 50$	$n = 57$	$n = 64$	$n = 71$
0	0,917497234	0,892700417	0,868575400	0,845102353	0,822263774	0,800041296	0,778419286	0,757382982
1	0,079156582	0,101522897	0,122622535	0,142507377	0,161228067	0,178832603	0,195367937	0,210878883
2	0,003259391	0,005573806	0,008415267	0,011735911	0,015490552	0,019636552	0,024133717	0,028944153
3	0,000085212	0,000196723	0,000374011	0,000628983	0,000971955	0,001411776	0,001955933	0,002610635
4	0,000001587	0,000005014	0,000012100	0,000024666	0,000044786	0,000074741	0,000116972	0,000174043
5	0,000000022	0,000000098	0,000000304	0,000000754	0,000001616	0,000003107	0,000005505	0,000009146
6		0,000000002	0,000000006	0,000000019	0,000000048	0,000000105	0,000000212	0,000000394
7					0,000000001	0,000000003	0,000000007	0,000000014

that the found discrepancy between expectation and estimation may be exceeded by pure chance in somewhat more than 20 cases out of 100. The discrepancy is, therefore, not significant.

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ZYTOLOGISCHE STUDIEN ÜBER DEN F_1-BASTARD TRITICUM TURGIDUM × SECALE CEREALE

VON *ALF LILJEFORS*
STOCKHOLM

(With a summary in English)

EINLEITUNG.

WÄHREND eines Aufenthalts in Svalöf im Sommer 1933 fixierte ich Material zum Studium der Mikrosporogenese einiger F_1-Bastarde zwischen *Triticum turgidum* und *Secale cereale*. Im folgenden Sommer wurde die Untersuchung ebendaselbst durchgeführt. Die Bastarde waren in der zytogenetischen Abteilung des Schwedischen Saatzuchtvereins hergestellt und wurden mir vom Vorstand, Herrn Dozent Dr. A. MÜNTZING, zur Verfügung gestellt. Ihm und dem Assistenten, Herrn Agronom Cand. phil. ROBERT LAMM, sage ich meinen besten Dank für geleistete Hilfe. Meinem verehrten Lehrer, Herrn Professor Dr. O. ROSENBERG bin ich auch zu grossem Dank verpflichtet für das Interesse, das er der Untersuchung stets zuteil werden liess. — Geldlich wurde die Arbeit durch ein Stipendium aus »Letterstedts inrikes resestipendiefond» unterstützt.

Die Bastarde, die von MÜNTZING (1935) beschrieben worden sind, repräsentierten folgende Sortenkombinationen:

Bastard A: *Trit. turgidum* var. *dinurum* × »Sangaste»-Roggen.
» B: *Trit. turgidum* var. *lusitanicum* × »Midsommar»-Roggen.

Die somatische Chromosomenzahl war bei beiden, wie erwartet, 21 (14 von *Tr. turgidum* + 7 von Roggen).

In zytologischer Hinsicht verhielten sich die beiden Bastarde ganz verschieden. Der Bastard A zeigte ein für Weizen—Roggen-Bastarde ungefähr normales zytologisches Bild, während der Bastard B sich ganz anders verhält. Ich habe sie daher im folgenden getrennt behandelt.

Als Fixierungsmittel ist NAVASHINS Formalin-Chromsäure-Eisessig (von MÜNTZING [1932] modifiziert) verwendet worden. Die Schnitte wurden 25 μ dick geschnitten und mit NEWTONS Gentianaviolett gefärbt.

I. TRITICUM TURGIDUM VAR. DINURUM × »SANGASTE»-ROGGEN (BASTARD A).

1. BEOBACHTUNGEN.

Die Prophasen waren nicht so gut fixiert, dass ich sie hätte studieren können. In der 1. Metaphase sind zumeist 1—2 Bivalente vorhanden. Die Anzahl variiert ziemlich stark: 0 bis 6 sind beobachtet worden (Fig. 1—5). Die Frequenz von P.M.Z. mit verschiedener Anzahl von Bivalenten ergibt sich aus folgender Übersicht.

Anzahl Bival. ..	0	1	2	3	4	5	6
» P.M.Z. ..	20	32	36	12	3	2	2; Summe 107.

Das macht im Durchschnitt 1,6 Bival./Zelle. Ziemlich oft, in ungef. 4 % der P.M.Z., kommt ein Trivalent vor. (Die Trivalente sind in der Übersicht als Bivalente behandelt.) Sie sind immer V-förmig und erscheinen nur einzeln in jeder Zelle, zusammen mit $1—5_{II}$ (Fig. 6—8). $1_{III} + 5_{II}$ ist also die maximale Bindung, die ich gesehen habe. — In zwei dicht aneinander liegenden P.M.Z. ist auch ein Tetravalent beobachtet worden (Fig. 9); es war in beiden Fällen zickzackförmig.

Die Bivalente sind gewöhnlich stabförmig; zuweilen kommt ein ringförmiges vor, aber nie mehr als eines in jeder P.M.Z. (Fig. 3 und 6). Die Chiasmen sind in der Regel terminal. Ein einziges Mal habe ich ein deutlich interstitielles Chiasma gesehen (Fig. 10). Das Aussehen der stabförmigen Bivalente variiert sehr, indem es ausser durch die Chiasmen auch durch den Dehnungsgrad bedingt ist. Dieser ist bisweilen, wie es scheint, abnorm (Fig. 11 *a*, die 3 Bival. von derselben P.M.Z. zeigt, Fig. 11 *b—e*). Gewöhnlich hat nur der eine Partner eines Bivalents diese Ausdehnung. Oft konnte ich gar keinen Chromatinfaden zwischen den beiden Teilen eines Chromosoms entdecken, trotzdem ich die Präparate stark gefärbt hatte (Fig. 11 *c—e*). Ähnliche defekte Chromosomen sind auch von HÅKANSSON (1930, S. 48) bei Speltoidheterozygoten und von MICZYNSKI (1931, S. 66) bei *Aegilops*-Bastarden beobachtet worden. — Die Univalente verteilen sich während der 1. Metaphase unregelmässig über die Spindel (Fig. 1—9). Auch können in Ausnahmefällen alle in der Äquatorialebene oder an den Polen liegen (Fig. 12).

Während der Anaphase wird die Längsteilung der Chromosomen sehr deutlich (Fig. 13). Die Bivalentchromosomen wandern zuerst nach den Polen, im allgemeinen ohne Störungen. Ausnahmsweise kann ein Chromatidenpaar Schwierigkeiten bei der Trennung haben (Fig. 15—17). Fig. 17 zeigt die eine von zwei nebeneinanderliegenden Zellen mit

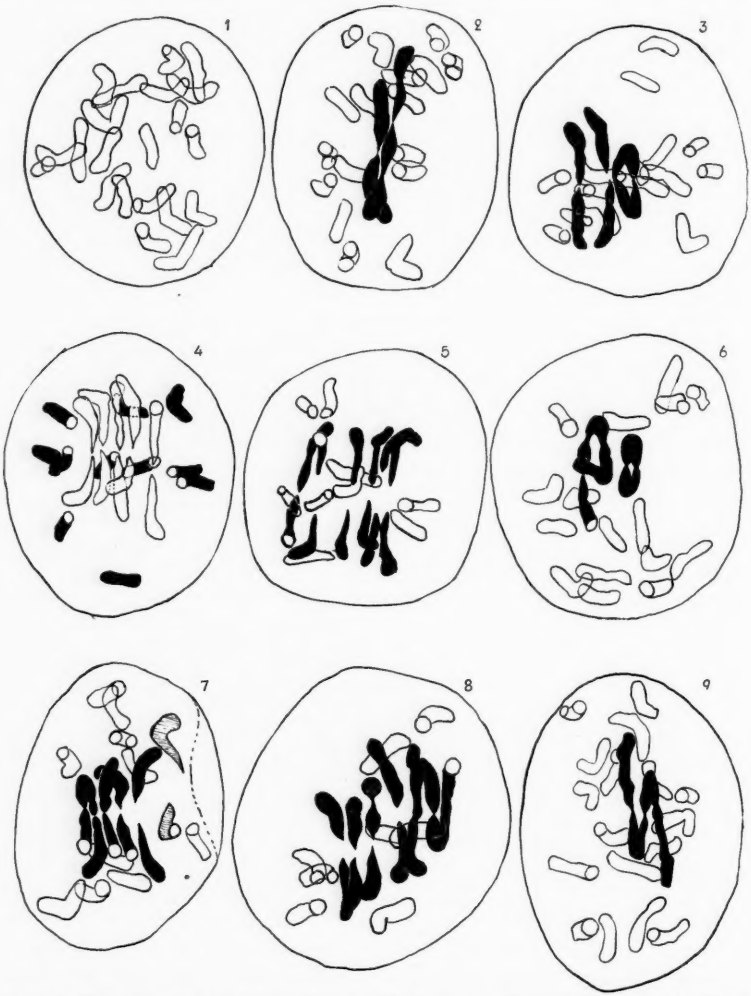

Fig. 1—9. *Triticum turgidum* var. *dinurum* × »Sangaste»-Roggen (Bastard A). Erste Metaphase. — Fig. 1. 21_I. — Fig. 2. $2_{II} + 17_I$. — Fig. 3. $3_{II} + 15_I$. — Fig. 4. $5_{II} + 11_I$. — Fig. 5. $6_{II} + 9_I$. — Fig. 6. $1_{III} + 1_{II} + 16_I$. — Fig. 7. $1_{III} + 4_{II} + 10_I$. — Fig. 8. $1_{III} + 5_{II} + 8_I$. — Fig. 9. $1_{IV} + 17_I$. — Vergr. ca. 2000.

ungefähr demselben Aussehen: das eine Chromatidenpaar war zu einer Brücke ausgezogen und unweit davon lag ein Fragment. Diese gleichzeitige Bildung einer Chromatinbrücke und eines Fragments ist neulich

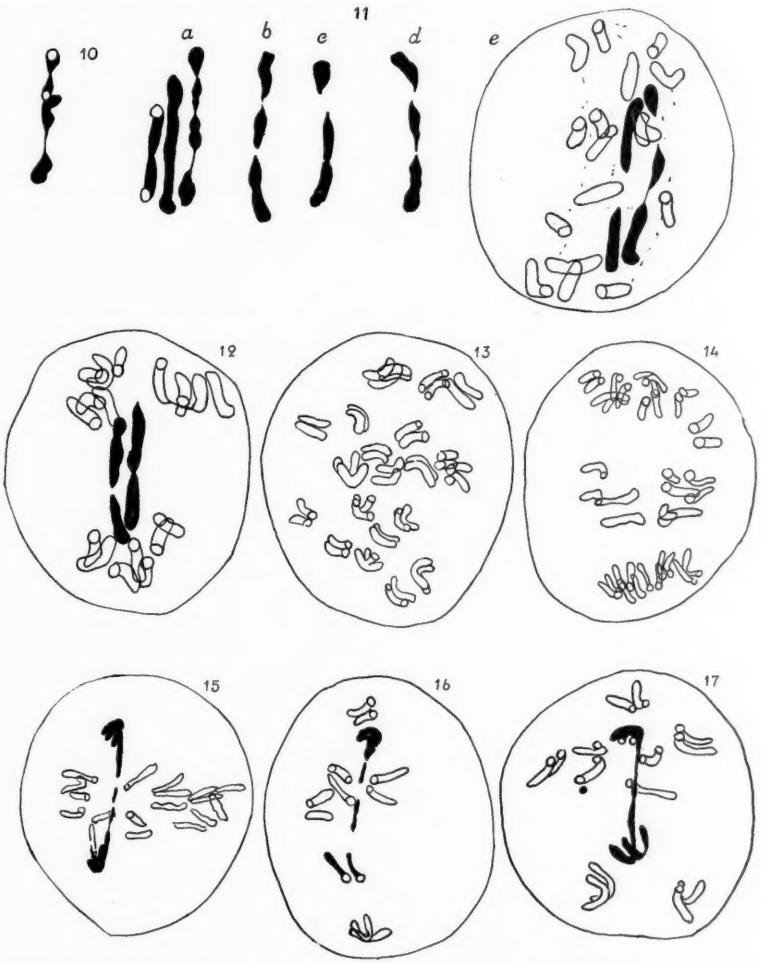

Fig. 10—17. *Triticum turgidum* var. *dinurum* × »Sangaste»-Roggen (Bastard A). — Fig. 10—12. Erste Metaphase. — Fig. 10. Geminus mit einem interstitiellen Chiasma. — Fig. 11 *a—e*. Bivalente aus verschiedenen P.M.Z., abnorme Einschnürungen (oder Fragmentierungen?) zeigend. — Fig. 12. Alle Univalente schon vor der Anaphase an den Polen. — Fig. 13—17. Erste Anaphase. — Fig. 13. Frühe Anaphase. 2_{II}. — Fig. 14. Späte Anaphase; sich teilende Univalente noch am Äquator. — Fig. 15—16. Fragmentbildung durch Reissen einer Chromatinbrücke. — Fig. 17. 1_{II}, dessen eines Chromatidenpaar zu einer Brücke ausgezogen ist; nebenan ein Fragment. — Vergr. ca. 2000.

sowohl von Mc Clintock (1933) wie von Müntzing (1934) beschrieben worden. Diese beiden Autoren erklären die Erscheinung als eine Folge von »crossing-over» zwischen zwei homologen Segmenten, von denen das eine invertiert ist: dabei entsteht ein Chromatid mit zwei »attachment points» und ein Fragment ohne »attachment point». Müntzing hat ausführlich verschiedene Möglichkeiten für diesen Fall besprochen, weshalb ich auf seine Abhandlung verweise. Vielleicht ist dies ein neues Beispiel dafür. In den beiden übrigen abgebildeten Fällen dürfte wohl die Ausdehnung auf ein schwerlösliches Chiasma zurückzuführen sein. Wahrscheinlich können Fragmentierungen eintreffen, wenn der Chromatinfaden zerreisst. — Von den Univalenten teilen sich hiernach die, die sich in der Äquatorialebene oder in unmittelbarer Nähe derselben befinden (Fig. 14). Die übrigen gehen ungeteilt nach den Polen. Verhältnismässig oft sieht man ein Univalent im Plasma, das ausserhalb der Spindel liegen bleibt (Fig. 18). Solche Univalente werden später zu Zwergkernen. Auch in der Spindel bleiben während der Telophase und Interkinese Chromatinelemente zurück, an Zahl zwischen 1 und 4 schwankend. Hier eine Übersicht:

Anzahl Chromatinkörper	0	1	2	3	4	
» Zellen	116	27	13	5	1	Summe 162.

Zu einem kleinen Teil dürften wohl diese Chromatinelemente aus geteilten Univalenten, d. h. Chromatiden bestehen; dazu sind jedoch die meisten allzu klein und müssen daher wahre Fragmente darstellen. Da ich in der 1. Metaphase nie Fragmente gesehen habe, müssen sie während der Anaphase gebildet worden sein. Wie dies geschehen kann, dafür haben wir neulich ein paar Beispiele gesehen: teils bei »crossing-over» zwischen invertierten Segmenten, und teils wenn eine Chromatinbrücke zerreisst. Indessen dürfte man wohl auch damit zu rechnen haben, dass die früher beschriebenen Bivalentchromosomen mit abnormen Einschnürungen zerreissen können und zur Entstehung von Fragmenten Anlass geben. Hierbei sind 2 gleich grosse Fragmente zu erwarten, da ja eine ev. Fragmentierung in diesem Stadium beide Chromatiden treffen muss. Sie müssen auch auf derselben Seite der neugebildeten Zellwand liegen. Fig. 19—21 zeigen Zellen, in denen diese Bedingungen erfüllt sind. — Hicks und Stebbins (1931, S. 238) haben bei *Paeonia* in der Meiosis Fälle mit 2 »sister-fragments» gefunden. Ihrer Meinung nach sind sie durch Bruch in einem ganzen Chromosom während der Anaphase entstanden, was meine Auffassung des vorliegenden Falles stützt. — Fig. 22 zeigt einen sonderbaren Fall, wo ein

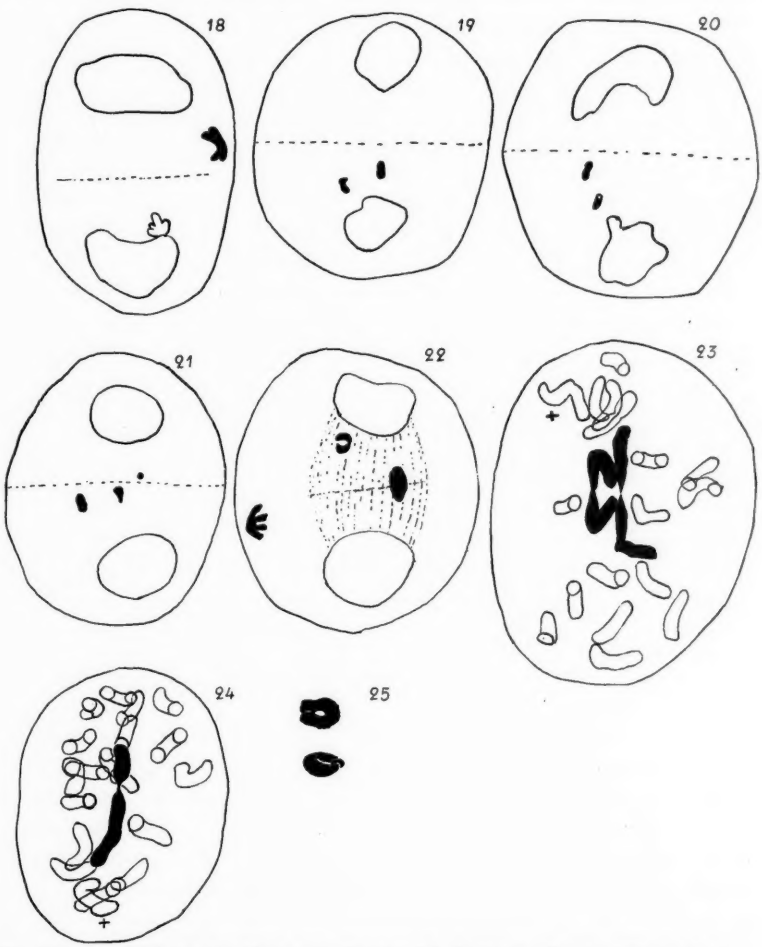

Fig. 18—25. *Triticum turgidum* var. *dinurum* × »Sangaste»-Roggen (Bastard A). — Fig. 18—22. Erste Telophase. — Fig. 18. Ein ungeteiltes Univalent ist im Plasma zurückgeblieben. — Fig. 19—21. Telophasen mit zwei ung. gleichgrossen Fragmenten an derselben Seite der Zellwand. — Fig. 22. Ein Univalent im Plasma und ein grosses Chromosomenstück noch am Äquator, wo es wahrscheinlich durch die Wand amputiert wird. — Fig. 23—24. Heteromorphe Bivalente. — Fig. 25. Ringförmige Univalente. — Vergr. ca. 2000.

grosser Chromatinkörper, vielleicht ein ungeteiltes Univalent, in der Spindel zurückgeblieben ist und dort durch die Wand wahrscheinlich amputiert wird.

Um ein ev. Vorkommen von Restitutionskernen nach der 1. Reifeteilung zu ermitteln, wurde eine Analyse von 125 P.M.Z. während der Interkinese ausgeführt. Sie ergab aber ein negatives Resultat: 112 waren in 2 Zellen geteilt, 13 hatten dennoch eine kleine dritte Zelle. — Von den homotypen Teilungen habe ich leider keine guten Präparate bekommen. Eine Analyse der Anzahl Zellen der »Tetraden» ergab Folgendes:

Anzahl Zellen	3	4	5	
» »Tetraden»	3	112	8;	Summe 123.

Die ganz überwiegende Anzahl P.M.Z. wird also, was die Zellenzahl betrifft, zu normalen Tetraden.

Ausser der früher erwähnten gleichzeitigen Bildung von Fragment und Chromatid mit doppelter Polfadeninsertion habe ich ein paar Fälle gesehen, die auf chromosomale Umlagerungen hindeuten: es sind das teils heteromorphe Bivalente (Fig. 23 und 24), teils ringförmige Univalente (Fig. 25).

Heteromorphe Bivalente können ja auch aus der Verbindung morphologisch verschiedener Chromosomen gebildet werden. In diesem Fall dürfte aber eine strukturelle Veränderung die Ursache sein, jedenfalls bei Fig. 24, wo der kleinere Partner deutlich kleiner ist als irgendein anderes Chromosom im Kern.

2. DISKUSSION.

Es ist ein Hauptproblem bei Bastarden vorliegender Art bestimmen zu können, inwieweit die Gemini durch Autosyndese oder durch Allosyndese gebildet sind, in diesem Fall also ob Chromosomen der *turgidum*-Genome A und B sich untereinander, oder ob Roggenchromosomen sich mit Weizenchromosomen gepaart haben, oder ob beides der Fall ist.

Autosyndese zwischen Weizenchromosomen ist mehrmals nachgewiesen worden. Da sind zuerst einige Beispiele von sicherer Autosyndese zwischen den A- und B-Genomen zu nennen. JENKINS (1929) fand beim Bastard *Tr. turgidum* (14) × *Aegilops speltoides* (7) bis zu 10 Bivalente. Hier müssen also mindestens 3 Gemini von *turgidum*-Chromosomen stammen. [Aber nicht von einem und demselben Genom, wie JENKINS selbst und später SCHIEMANN (1932) annehmen, sondern von verschiedenen Genomen, gemäss den Schemata von KIHARA und LILIENFELD (1932, S. 403) oder DARLINGTON (1932, S. 147).] KIHARA u. LILIENFELD (1932, S. 401) haben bei der Kreuzung *Tr. durum* × *Aeg.*

Aucheri bis 5, wahrscheinlich 6, Trivalente beobachtet. Sie schreiben darüber: »Nach dem Konjugationsbilde des vorliegenden Bastards zu urteilen, würden sich die intergenomatischen Beziehungen S (= *Aegilops Aucheri*-Genom)—A_{Em}, S—B_{Em} und wahrscheinlich auch A_{Em}—B_{Em} ähnlich gestalten, wenn entsprechende Verbindungen (SA_{Em}, SB_{Em} und $A_{Em}B_{Em}$) möglich wären. Die volle Anzahl der realisierbaren Verbindungen zwischen je 2 Genomen kann man danach als 7 annehmen; im extremen Fall könnten also bei unserem Bastard 7_{III} gebildet werden. Gefunden wurden höchst wahrscheinlich 6, ganz sicher 5».

KIHARA und NISHIYAMA (1930) haben bei ihren eingehenden Untersuchungen der Weizengenome festgestellt, dass sowohl zwischen den Genomen A und B wie zwischen B und C (D-Genom laut KIHARA) 2—3 Bivalente vorkommen können.

Weitere Fälle von Autosyndese bei Weizenchromosomen sind folgende. Bei haploidem *Triticum compactum* wurden bis zu 3 Bivalente gefunden (GAINES und AASE, 1926). In einer F_2-Pflanze, durch Rückkreuzung des Bastards *Tr. vulgare* (21) × *Secale* (7) mit *Secale* entstanden, fand LEBEDEFF (1932) die Kombination $14_{II} + 7_{I}$; hier müssen mindestens 7 Gemini von Autosyndese der Weizenchromosomen herrühren.

Obenstehende Untersuchungen zeigen also, dass durch Autosyndese zwischen den Genomen des Haploidsatzes von tetraploidem Weizen 5, wahrscheinlich 6, und von hexaploidem Weizen 7 Bivalente gebildet werden können.

Vergleichen wir diese Angaben über Autosyndese innerhalb der *Triticum*-Genome mit der Paarung in Weizen—Roggen-Bastarden (Tab. 1), so finden wir, dass die Paarung bei diesen sich nicht auf mehr Chromosomen erstreckt als sich autosyndetisch binden können. (Vgl. KIHARA und NISHIYAMA, 1930.) Somit müssen wir sagen, dass die Möglichkeit gegeben ist, auch die Chromosomenbindung der Weizen—Roggen-Bastarde als Autosyndese zu erklären. Nur bei vorliegender Kreuzung ist die maximale Bindung, $5_{II} + 1_{III}$, ein wenig höher als die früher sicher beobachtete Autosyndese bei dem Haploidsatz von tetraploidem Weizen. KIHARA und LILIENFELD (a. a. O.) konnten »höchst wahrscheinlich 6, ganz sicher 5» wahrnehmen. Sie glauben aber, dass die maximale Bindung sich auf alle 7 Chromosomenpaare erstrecken kann. Mit Rücksicht hierauf und da die Chromosomenbindung bei allen anderen Weizen—Roggen-Bastarden sich autosyndetisch erklären lässt, muss man annehmen können, dass dies auch beim vorliegenden Bastard der Fall ist.

TABELLE 1. *Chromosomenbindung in F_1-Weizen—Roggen-Bastarden.*

durum	14	*cereale*	$0—4_{II}$				AASE, 1930
dicoccoides	»	*montanum*	$0—1_{II}$				LONGLEY und SANDO, 1930
durum	»	*cereale*	$0—5_{II}$				KAGAWA und CHIZAKI, 1934
turgidum	»	»	$15—21_{I}$	$0—6_{II}$	1_{III}	1_{IV}	LILJEFORS
vulgare	21	»	$0—3_{II}$				KIHARA, 1924; THOMPSON, 1926
»	»	»	$0—3_{II}$				AASE, 1930
»	»	»	$0—4_{II}$				BLEIER, 1930
»	»	»	0_{II}				LONGLEY und SANDO, 1930
»	»	»	$0—3_{II}$				FLORELL, 1931
»	»	»	$0—2_{II}$				BLEIER, 1933
»	»	»	$14—28_{I}$	$0—6_{II}$	$1—2_{III}$		KATTERMANN, 1934
»	»	»	$20—28_{I}$	$0—4_{II}$	1_{III}		KATTERMANN, 1934
»	»	*montanum*	$0—1_{II}$				LONGLEY und SANDO, 1930
spelta	»	*cereale*	$0—4_{II}$				AASE, 1930; KAGAWA und CHIZAKI, 1934
»	»	*montanum*	$0—3_{II}$				LONGLEY und SANDO, 1930
compactum	»	*cereale*	$0—3_{II}$				KAGAWA und CHIZAKI, 1934

Dennoch hat PLOTNIKOWA (1930) zwei triploide Weizen—Roggen-Bastarde untersucht. Sie behauptet keine deutlichen Bivalente gefunden zu haben. Ihre Untersuchung ist jedoch, wie sie selbst sagt, unvollständig, und ihre Bilder zeigen, dass Bivalente wahrscheinlich vorkommen.

Damit ist aber nicht gesagt, dass Allosyndese ausgeschlossen ist. Das zytologische Bild bei der vorliegenden Kreuzung gibt hierüber keine sichere Auskunft. v. BERG (1931) konnte bei der Kreuzung *Aegilops triuncialis* × *Secale cereale* auf Grund des Grössenunterschiedes der Chromosomen der verschiedenen Eltern feststellen, dass nur Autosyndese der *Aegilops*-Chromosomen vorkam. Das ist hier leider nicht möglich, da die Grössenunterschiede, obwohl vorhanden, doch nicht genügend ausgesprochen sind.

Eine Sache, die aber am ehesten gegen Allosyndese spricht, ist der Umstand, dass die Anzahl gebundener Chromosomen immer kleiner als 14 ist. Im entgegengesetzten Falle sollte man erwarten, dass irgendeinmal mehr als 14 Chromosomen in Bindungen, Bi- oder Trivalenten,

enthalten sein sollten, wie dies bei den triploiden Weizen-*Aegilops*-Bastarden der Fall ist (JENKINS, 1929; KIHARA und LILIENFELD, 1932). Das Vorkommen von ringförmigen Gemini spricht auch für Autosyndese.

In den Fällen, wo ein deutliches heteromorphes Bivalent vorkommt, ist die Ursache zur Bildung desselben so gut wie sicher eine Translokation. KAGAWA und CHIZAKI (1934, S. 30) berichten über »bipartite chromosomes» bei der Kreuzung *Tr. durum* × *Secale cereale*; auch sie sind der Ansicht, dass sie durch Translokation entstanden sind. — In bezug auf die unzweifelhaft starke Autosyndese und auf das Vorkommen von Translokationen sind wohl auch die Multivalente als ausschliesslich durch Autosyndese gebildet anzusehen. Jedenfalls sind sie kein Beweis für Allosyndese.

Das kräftigste Argument gegen ein Vorkommen von Allosyndese bei Weizen—Roggen-Bastarden liefern aber die Ergebnisse der ziemlich zahlreichen zytogenetischen Untersuchungen der Nachkommenschaft von solchen, die mit Weizen rückgekreuzt sind (bezüglich Literatur siehe BLEIER, 1933). Abgesehen von Amphidiploiden und noch nicht konstanten Individuen mit unbalanzierten Chromosomenzahlen, ist es noch nicht gelungen, Weizen- und Roggen-Eigenschaften zu vereinigen. Dies trifft also nur dann ein, wenn ganze Roggenchromosomen unter den Weizenchromosomen vorhanden sind. Linien mit 42 Chromosomen sind immer reine Weizenlinien, folglich kann kein Genaustausch mit Roggen stattgefunden haben, d. h. zwischen Weizen- und Roggenchromosomen hat keine Paarung stattgefunden. Vielleicht muss man damit rechnen, dass ein durch »crossing-over» verändertes Weizenchromosom bei der Paarung mit seinem Homologen Schwierigkeiten haben kann und daher eliminiert wird. Es ist aber kaum wahrscheinlich, dass dies immer der Fall sein wird, auch bei wenig veränderten Chromosomen.

Auf Grund des oben Gesagten *halte ich es für wahrscheinlich, dass die Gemini und Multivalente bei der vorliegenden Kreuzung ausschliesslich durch Autosyndese der turgidum-Chromosomen gebildet sind.* Die Gründe hierfür fasse ich folgendermassen zusammen:

1) Die Autosyndese, die bei Weizengenomen vorkommen kann, ist genügend gross, um die Chromosomenbindungen bei allen bisher untersuchten Weizen—Roggen-Bastarden, den vorliegenden ausgenommen, autosyndetisch erklären zu können.

2) Die zytogenetischen Untersuchungen von mit Weizen rückge-

kreuzten Weizen × Roggen-Bastarden zeigen, dass kein Genaustausch zwischen Weizen- und Roggenchromosomen vorkommt.

3) Die zytologischen Verhältnisse beim vorliegenden Bastard, besonders der Umstand, dass immer weniger als 14 Chromosomen gebunden sind, sprechen am ehesten für Autosyndese.

MEISTER stellte 1927 die Hypothese auf, dass der hexaploide Weizen aus der Kreuzung *Trit. dicoccum* × Roggen abzuleiten wäre. Die spezifischen Eigenschaften des *vulgare*-Weizen sollten demnach vom Roggen herrühren. Die Chromosomen des »Extragenoms» im *vulgare*-Weizen, des C-Genoms, (D-Genom nach KIHARA), müssten in diesem Falle jedenfalls teilweise vom Roggen herstammen. Man würde dann erwarten, dass die Höchstzahl möglicher Bivalente bei den tetraploiden Weizen—Roggen-Bastarden mit der Genom-Konstitution A B C R grösser sein würde als bei den triploiden A B R (R = Roggengenom).

Ein Blick auf die Zusammenstellung auf Seite 248 der bisher untersuchten triploiden und tetraploiden Weizen—Roggen-Bastarden sagt uns, dass dies nicht der Fall ist. Die Höchstzahl beobachteter Bivalente in einer P.M.Z. ist sowohl bei triploiden als bei tetraploiden Bastarden, 6. Überdies scheint es, als ob die Geminifrequenz bei den triploiden Bastarden etwas höher sei. Die Anzahl untersuchter triploider Bastarde ist jedoch noch zu gering, um das entscheiden zu können. Jedenfalls muss man behaupten können, dass die Geminibildung bei den triploiden Bastarden nicht schwächer ist.

Somit muss MEISTERS Roggenhypothese aus zytologischen Gründen abgelehnt werden. Das haben schon früher SCHIEMANN (1932, S. 41) und LEBEDEFF (1932, S. 71) getan, aber nur auf Grund der schwachen Geminibildung der tetraploiden Bastarde und ohne diesen Vergleich mit den triploiden, der mir entscheidend scheint. Neulich ist MÜNTZING (1935, S. 158) durch ein Studium der Meiosis bei dem Trippelbastard (*Triticum turgidum* × *Secale cereale*) × *T. vulgare* zu demselben Schluss gekommen.

II. TRITICUM TURGIDUM VAR. LUSITANICUM × »MIDSOMMAR»-ROGGEN (BASTARD B).

1. BEOBACHTUNGEN.

Diese Kreuzung zeigt ein sehr eigentümliches zytologisches Bild, ganz verschieden von dem Bastard A und auch von allen anderen

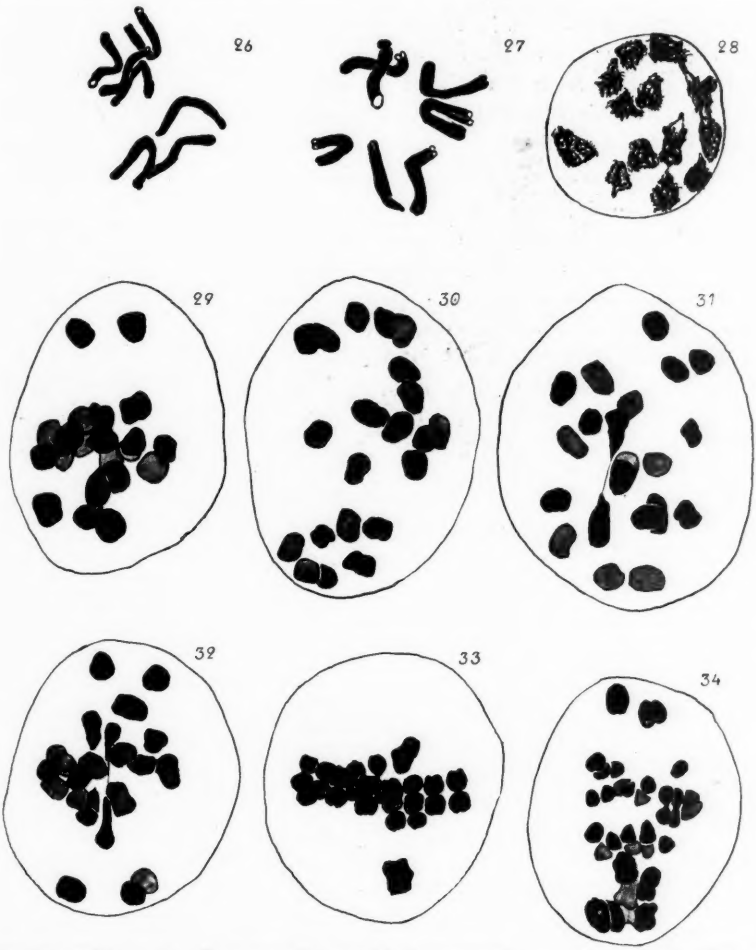

Fig. 26. *Triticum turgidum* var. *dinurum* × »Sangaste»-Roggen (Bastard A). Einige Chromosomen in Metaphase aus einer Mitose im Nuzellus. — Fig. 27—34. *Trit. turgidum* var. *lusitanicum* × »Midsommar»-Roggen (Bastard B). — Fig. 27. Einige Chromosomen in Metaphase aus einer Mitose im Nuzellus. — Fig. 28. Diakinese (unvollständig). Chromosomen kettenförmig geordnet. — Fig. 29—33. Erste Metaphase. Fig. 29—30. 21_I. — Fig. 31. $1_{II} + 19_I$. — Fig 32. $2_{II} + 17_I$. — Fig. 33. 21_I (unvollständig), nur zwei nicht am Äquator. — Fig. 34. Anaphase. — Vergr. ca. 2000.

früher untersuchten Weizen—Roggen-Kreuzungen. Das Merkwürdige bei dieser ist, dass die meiotischen Chromosomen abnorm stark kontrahiert sind, und zwar viel stärker als gewöhnlich in der Meiosis bei diesen

oder verwandten Arten. Ausserdem herrscht so gut wie vollständige Asyndese und die normale Gleichzeitigkeit der Teilungsstadien in einem und demselben Antherenfach ist gestört. Man kann durcheinander Zellgruppen oder vereinzelte Zellen in allen Entwicklungsstadien zwischen Diakinese und Tetrade antreffen. In allen P.M.Z. scheint aber die Meiosis durchgeführt zu werden, denn in etwas älteren Antherenfächern gibt es nur Tetraden. Diese degenerieren aber früh.

Die Chromosomen in der Mitose. — Die abnorme Kontraktion scheint nur in geringem Masse die mitotischen Chromosomen betroffen zu haben. Leider habe ich kein Wurzelspitzenmaterial untersuchen können, weshalb ein zuverlässiger Vergleich zwischen den Bastarden A und B erschwert worden ist. Man sieht aber ziemlich gut in Teilungen der Nuzelluszellen, dass die Chromosomen des vorliegenden Bastards B (Fig. 27) etwas dicker sind als die des Bastards A (Fig. 26). Der Unterschied ist aber gering und gar nicht so ausgeprägt wie in der Meiosis, und rührt vielleicht nur von Unterschieden in der Einwirkung des Fixierungsmittels her.

Beschreibung der Meiosis. — Schon in der Diakinese haben die Chromosomen die beinahe sphärische Form erreicht, die sie in der stärksten Kontraktion während der Metaphase haben. Fig. 28 zeigt ein Diakinesestadium (nicht alle Chromosomen sind eingezeichnet). Die Chromosomen haben in diesem Stadium eine alveolierte Struktur. Ihre Gruppierung ist auch bemerkenswert. Sie bilden oft lange, kettenähnliche Reihen, was einen sehr eigentümlichen Eindruck macht. Es scheint, als ob sie sich eher attrahierten, statt sich wie gewöhnlich zu repellieren. Mitunter kann man auch deutlich Chromatinkonnexe zwischen den einzelnen Chromosomen wahrnehmen. Fixierungsartefakte von natürlichen Konfigurationen hier zu unterscheiden, ist natürlich unmöglich. Es ist aber wohl kaum wahrscheinlich, dass das Fixiermittel allein solche Kettenbildungen verursachen kann.

In der Metaphase bleibt aber von diesen Verbindungen nichts übrig. Die Chromosomen sind hier beinahe kugelförmig. Ausnahmsweise kann ein kleiner Unterschied zwischen verschiedenen P.M.Z. bestehen, wie man bei einem Vergleich Fig. 29 und 32 sieht, was vielleicht nur vom Fixierungsmittel verursacht ist. Nachdem in der Telophase die Chromosomen aufgelöst worden sind, werden sie während der Interkinese wieder abnorm kräftig kontrahiert, so dass sie in der homotypen Teilung das Aussehen von Fig. 42 haben. Ein Vergleich mit dem entsprechenden Stadium beim Bastard A (Fig. 43) zeigt am besten den Kontraktionsgrad.

In M I herrscht meistens vollständige Asyndese (Fig. 29—30). Ausnahmsweise kommen 1, höchstens 2 Bivalente vor, deren Chromosomen etwas in die Länge gezogen sind (Fig. 31 und 32). Die Geminifrequenz geht aus folgender Übersicht hervor:

Anzahl Gemini	0	1	2	
» P.M.Z.	91	20	2;	Summe 113.

Im Durchschnitt also 0,2 Geminus pro P.M.Z. Multivalente habe ich nie gesehen.

Die Univalente liegen wie gewöhnlich über die Spindel zerstreut und verteilen sich sehr ungleichmässig nach den Polen hin. In der Regel wandern jedoch einige, ihre Anzahl kann sehr wechseln, zur Äquatorialebene und werden in M I geteilt (Fig. 34). Bisweilen liegen beinahe alle in der Äquatorialebene, wie in Fig. 33. Wahrscheinlich können ausnahmsweise sämtliche in M I geteilt werden. Die Anaphase ist gewöhnlich ziemlich regelmässig: 2 getrennte, aber allerdings oft ungleichgrosse Telophasengruppen werden gebildet (Fig. 35). Verhältnismässig selten bleiben vereinzelte Chromosomen oder Bruchstücke solcher im Plasma liegen (Fig. 36).

Es ist jedoch nicht Regel, dass die Teilung so verhältnismässig »normal», wie oben beschrieben, verläuft. Besonders in der Ana- und Telophase beobachtet man Abweichungen, wahrscheinlich von degenerativer Natur. Sich teilende Univalente werden fadenähnlich ausgezogen, und die ungeteilten klumpen sich zusammen (Fig. 37). Dies kann kein Fixierungsartefakt sein, denn das Plasma hat in jenen Zellen das gleiche Aussehen wie in der »normalen» P.M.Z. Offenbar sind die Chromosomen sehr viskos, und die Teilungshälften gehen nur schwer auseinander. Sie erinnern an die klebrigen (»sticky») Chromosomen, die BEADLE (1932) bei *Zea* beschrieben hat.

Diese Neigung der Chromosomen, sich zusammenzuklumpen, erscheint in verschiedenen Zellen verschieden ausgeprägt. In extremen Fällen scheint in der Anaphase keine ordentliche Aufteilung in zwei Gruppen stattgefunden zu haben, sondern alle Chromosomen bleiben in der Telophase zusammen liegen (Fig. 38). (Dass es sich hier wirklich um eine Telophase handelt, geht daraus hervor, dass die Chromosomen sich schon aufzulösen begonnen haben.) Wahrscheinlich ist hier auch der Spindelmechanismus von Degeneration betroffen. Interessant ist aber, dass eine deutliche Äquatorialebene ausgebildet ist, und man kann an dieser mit Sicherheit einige geteilte Univalente unterscheiden. Eine Teilung ist also in Gang gekommen, kann aber nicht durchgeführt

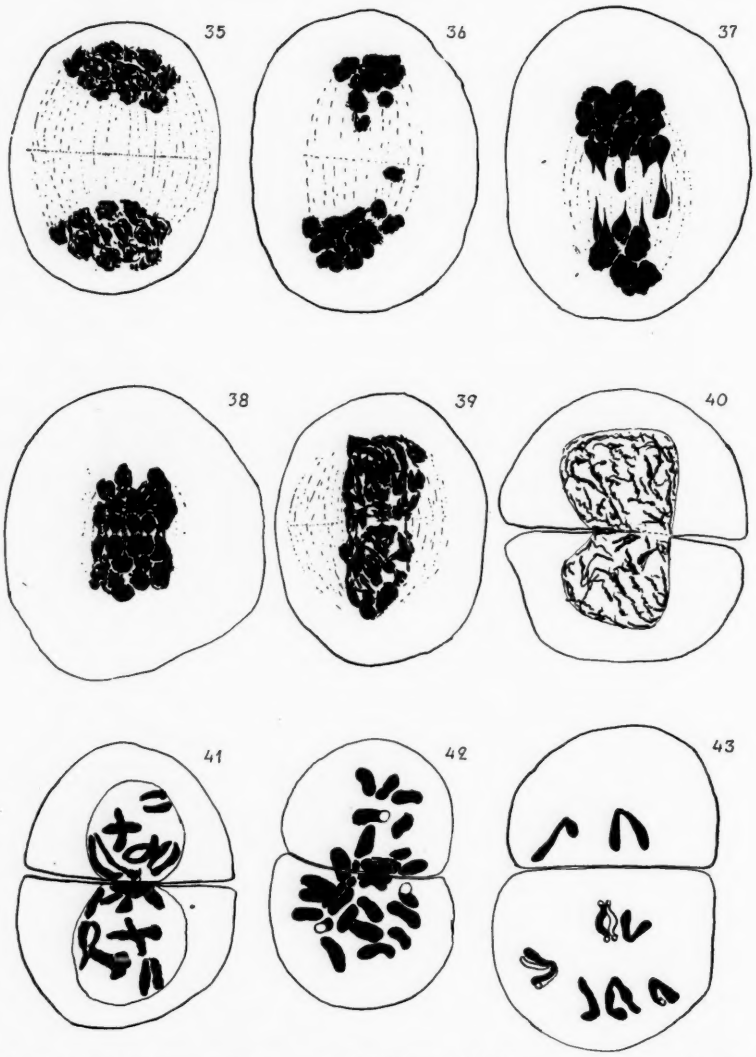

Fig. 35—42. *Triticum turgidum* var. *lusitanicum* × »Midsommar»-Roggen (Bastard B). — Fig. 35—36. Telophasen, »normal» (siehe den Text). Die Zellplatte wird vor der neuen Kernmembran angelegt. — Fig. 37. »Klebrige» Chromosomen. — Fig. 38—42. Die Entwicklung in den P.M.Z. mit degenerierter Anaphase. (Erklärung im Text S. 253). — Fig. 38—40. Verschiedene Telophasestadien. — Fig. 41. Interkinese. — Fig. 42. Zweite Metaphase. — Fig. 43. *Trit. turgidum* var. *dinurum* × »Sangaste»-Roggen (Bastard A). Einige Chromosomen aus einer zweiten Metaphase. — Vergr. ca. 2000.

werden. Fig. 39 zeigt ein späteres Telophasenstadium, wo es ganz unmöglich ist, einzelne Chromosomen zu unterscheiden. Auch hier kann man aber an der Mitte der Chromatinansammlung eine hellere Spalte, die Äquatorialebene, sehen.

Man kann folglich 2 verschiedene Typen von Telophasen unterscheiden: teils »normale» mit 2 Chromatingruppen, teils solche mit nur 1 Chromatingruppe. Die Frequenz der beiden Typen war in einer Blüte: P.M.Z. mit 1 Chromatingruppe 26, P.M.Z. mit 2 Chromatingruppen 22. (Zur Klasse 2 Chromatingruppen habe ich hierbei diejenigen P.M.Z. gerechnet, die einzelne Chromatinstücke im Plasma hatten.)

Man sollte ja vermuten, dass Restitutionskerne (ROSENBERG, 1927) und später Dyaden ziemlich allgemein nach Telophasen mit nur 1 Chromatingruppe gebildet würden. Im nächstfolgenden Stadium sieht man auch häufig restitutionskernähnliche Bildungen. In den allermeisten Fällen scheinen sie aber durch eine Wand quergeteilt zu sein (Fig. 40). Es ist schwer, um nicht zu sagen unmöglich, sicher zu entscheiden, ob die Wand wirklich »durch» den Kern geht oder die Kernmembran nur einschnürt. Die Chromosomen sind in diesem Stadium fadenähnlich und liegen im ganzen Kernraum als ein Chromatingerüst verteilt, was die Beobachtung erschwert. Später in der Interkinese kann man aber deutlich sehen, dass eine Wand zwei dicht aneinander liegende Kerne trennt (Fig. 41).

Wenn nun wirklich durch die Zytokinese eine Aufteilung einer in der Telophase einzeln vorkommenden Chromatingruppe in zwei Kerne und zwei Zellen stattgefunden hat, muss man das auch statistisch zeigen können, und zwar durch einen Vergleich der Häufigkeit von 1-zelligen P.M.Z. in M II mit der früher erwähnten Häufigkeit der P.M.Z. in T I mit nur einer Chromatingruppe. In derselben Blüte wie vorher betrug die Anzahl 1-zelliger P.M.Z. 17 und 2-zelliger 86. In Prozenten ausgedrückt gibt es in T I 54,2 % P.M.Z. mit 1 Chromatingruppe und in M II 15,4 % 1-zellige P.M.Z. Diese grosse Differenz zwischen korrespondierenden Gruppen zwingt zu derselben Annahme wie das zytologische Bild, nämlich dass eine Chromatingruppe in T I später durch einsetzende Wandbildung in zwei Kerne und Zellen aufgeteilt wird.

Wie ist ein so eigentümlicher Vorgang zu verstehen? Die Wandbildung in den P.M.Z. der Gräser ist bekanntlich sukzedan und erfolgt durch die Anlage einer sog. Zellplatte in der Äquatorialebene. Die Zellplatte wird unmittelbar nach der Anaphase angelegt (Fig. 35—36), also *bevor* noch eine Kernmembran rings um die Telophasechromosomen

ausgebildet ist. Wenn nun der normale zeitliche Zusammenhang zwischen Chromosom- und Zellteilung auch in Zellen mit gestörter Chromosomenteilung besteht, muss man annehmen können, dass die Zellplatte auch in der Spindel zwischen und in unmittelbarer Nähe von den Chromosomen angelegt werden kann. Wie schon erwähnt, kann man auch in den kompakten Chromatinanhäufungen im Telophasenstadium deutlich eine Äquatorialebene wahrnehmen, wenn sie auch nur eine sehr enge Spalte bildet. Eine Menge Chromatinfäden und auch einzelne Chromosomen kreuzen die Spalte. Sie ist aber eine verhältnismässig chromatinfreie Zone. Übrigens gibt es mehrere Beispiele dafür, dass die Zellplatte nachhinkende Chromosomen oder Chromatinfäden abschneiden kann [KATTERMANN (1930, S. 750) bei *Anthoxanthum*, MICZYNSKI (1931, S. 65) bei *Aegilops*, DARLINGTON (1932, S. 167) bei *Hyacinthus*]. Wenn wir also annehmen, dass eine Zellplatte angelegt wird, dann muss sie verhindern, dass die später sich bildende Kernmembran ununterbrochen die ganze Chromatinmasse umschliesst. Statt dessen werden zwei Kerne gebildet, einer an jeder Seite der Zellplatte. Diese werden durch die hier angenommene Bildungsart an den einander zugekehrten Seiten abgeplattet, und der ganze Komplex macht den eigentümlichen Eindruck von zweigeteilten Restitutionskernen, so wie man dies in den Fig. 40 und 41 sieht. Zwar scheinen diese Komplexe mehr oder weniger von der Zellwand eingeschnürt zu sein, besonders im Interkinesenstadium. Ein solches Bild muss aber auch entstehen, wenn der Telophasenkern ausgespannt und abgerundet wird. Oft ist auch die Chromatinmasse schon in früher Telophase mehr oder weniger hantelförmig (Fig. 39).

Nach diesem Erklärungsversuch wird also in den obengenannten Fällen kein Restitutionskern gebildet, sondern es werden von Anfang an zwei getrennte, aber dicht aneinander liegende Kerne gebildet. Der Vorgang zeigt, wie unabhängig voneinander Kern- und Zellteilung sind.

Wie bereits erwähnt, kommen auch wirkliche Restitutionskerne vor (Fig. 44—46). Zuweilen hat die Zellwand nur ein Stück Plasma abgeschieden (Fig. 46).

In der homotypen Teilung bekommt man einige eigentümliche Bilder zu sehen, die ein Resultat der soeben besprochenen Teilungsart sein müssen. Sowohl in Polansicht wie in Seitenansicht sieht die Metaphase oft wie eine Platte aus, obwohl die Wand quer hindurchgeht (Fig. 42). Dass mehrere Chromosomen in beiden Zellen dicht neben der trennenden Wand liegen ist wohl kein Zufall, sondern vielmehr eine Folge der Wandbildung an dieser Stelle. Man kann auch die schon

bekannte Tatsache beobachten, dass die Chromosomen während der Interkinese untereinander die Lage nicht verändern. Wie könnte man sonst erklären, dass mehrere Chromosomen in den beiden Zellen genau einander gegenüber liegen! Dies ist wahrscheinlich ein Folgestadium solcher Stadien, die in den Fig. 38—41 abgebildet sind.

Im übrigen verläuft die 2. Teilung, wie es gewöhnlich der Fall ist, wenn einige Univalente in der 1. Teilung gespalten worden sind. Eine Analyse der Tetraden (in derselben Blüte wie bei den früheren statistischen Berechnungen) gab folgendes Resultat:

Anzahl Zellen	2	3	4	5	
» Zellgruppen	8	6	105	1;	Summe 120.

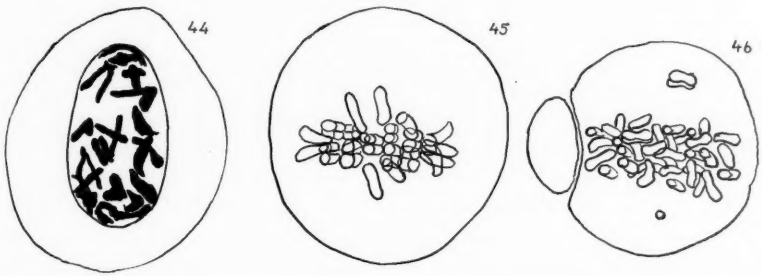

Fig. 44—46. *Triticum turgidum* var. *lusitanicum* × »Midsommar»-Roggen (Bastard B). Restitutionskerne. — Fig. 44. Interkinese. — Fig. 45—46. Zweite Metaphase. — Vergr. ca. 2000.

2. DISKUSSION.

Es sind zwei Sachen, die bei diesem Bastard in zytologischer Hinsicht besonders beachtenswert sind: teils die Asyndese, teils die abnorme Kontraktion der meiotischen Chromosomen. Oben haben wir gesehen, dass beim Bastard A bis 6 Bivalente in der 1. Metaphase vorkommen, und dass diese mit grösster Wahrscheinlichkeit ausschliesslich durch Autosyndese zwischen den *turgidum*-Genomen gebildet worden sind.

Der Unterschied in dieser Beziehung zwischen zwei Sorten derselben *Triticum*-Art ist also beträchtlich. Man kann unmöglich annehmen, dass so grosse Ungleichheiten bezüglich der Homologie der beiden Genomen bei zwei Sorten derselben Art vorhanden sind, dass diese allein für den Unterschied in der Paarung verantwortlich sein können. Wir müssen somit schliessen, dass es beim Bastard B nicht mangelnde Homologie, sondern etwas anderes ist, das die Asyndese

verursacht. Man muss sich da ein spezielles Gen oder eine spezielle Genkombination für die Asyndese denken. Vielleicht können auch Milieueinflüsse in Frage kommen.

Ein Beispiel von Pflanzen oder Tieren, bei denen die Chromosomen in der Meiosis stärker als normal kontrahiert sind, ist meines Wissens bisher nicht bekannt. Meine Studien des hier vorliegenden Falles beschränken sich auf die Stadien zwischen Diakinese und Tetrade. Beobachtungen einer ev. Pachytänpaarung oder Chiasmabildung konnten nicht vorgenommen werden. Auch ist die Zytogenetik der Pflanze unbekannt. Es sagt sich da von selbst, dass ein Versuch, die hier erwähnten Verhältnisse zu erklären und zueinander in Beziehung zu setzen, rein hypothetischen Charakter haben muss. Es ist nur möglich, einige Annahmen im Anschluss an früher bekannte Tatsachen zu machen.

Man kann sich zwei Möglichkeiten denken. Sowohl Asyndese wie Chromosomenkontraktion können jede für sich, unabhängig voneinander, durch ein Gen bedingt sein. Oder sie können beide Äusserungen eines und desselben Gens oder Genkomplexes sein und ev. in Kausalzusammenhang miteinander stehen.

Stellen wir uns zuerst den Fall vor, dass sowohl Asyndese wie Chromosomenkontraktion jede für sich durch ein Gen bedingt sind. Es ist da festzustellen, dass ähnliche Fälle wie der vorliegende betreffs der Chromosomenkonjugation bekannt sind. Die bekannten Beispiele *Digitalis lutea* (HAASE-BESSEL, 1922) und *Chrysanthemum marginatum* (SHIMOTOMAI, 1931) sind zu nennen, bei denen die Chromosomen bei derselben Art in einer Kreuzung volle oder hohe Autosyndese, in einer anderen aber Asyndese zeigen. Offenbar ist die Asyndese im letzteren Falle durch eine spezielle Genkombination verursacht. Weder bei diesen noch bei anderen Beispielen von genbedingter Asyndese, wie *Datura* (BLAKESLEE, 1928), *Zea* (BEADLE, 1930), *Viola* (CLAUSEN, 1930), *Hordeum* (EKSTRAND, 1932) treten Störungen in der Chromosomenkontraktion auf.

Andererseits ist ein Beispiel von genetisch bedingter Veränderung der Chromosomenkontraktion, ohne aber mit Störungen in der Paarung verbunden zu sein, von einem Schmetterling, *Phragmatobia*, bekannt (SEILER, 1925). Von diesem kommt eine Rasse vor mit sowohl in der Mitose als in der Meiosis konstant längeren Chromosomen als den normalen. Ähnlich verhält sich ein Individuum in F_3 der Kreuzung *Viola tricolor* × *V. orphanidis* (CLAUSEN, 1930): die Chromosomen sind sowohl in der Mitose als in der Meiosis konstant länger als gewöhnlich. Keiner

von diesen Fällen stimmt also mit dem vorliegenden *Triticum* × *Secale*-Bastard überein, wo die Chromosomen stärker kontrahiert, also kürzer als gewöhnlich sind.

Die obenstehenden Beispiele zeigen aber, dass sowohl Asyndese wie Veränderungen in der Chromosomenkontraktion genbedingt sein können. Man könnte dann annehmen, dass hier eine Genkombination vorläge, die teils die Asyndese und teils die abnorme Chromosomenkontraktion bedingt. Es scheint mir aber wenig wahrscheinlich, dass zwei so äusserst seltene Erscheinungen zufälligerweise zusammenangetreten sein sollten, ohne nähere Beziehung zueinander zu haben.

DARLINGTON (1932) vermag mittelst seiner »Precocity»-Theorie in mehreren Fällen eine Erklärung für das gleichzeitige Auftreten in der Meiosis von Unregelmässigkeiten in der Konjugation und Kontraktion der Chromosomen zu geben. Sie werden beide auf dieselbe Ursache zurückgeführt und zwar auf eine Veränderung des (in der Theorie postulierten) normalen Zeitunterschiedes zwischen Beginn der Prophase und der Chromosomenteilung. Zufolge dieser Theorie muss aber eine verminderte Kontraktion zusammen mit reduzierter Paarung auftreten, wie z. B. in *Matthiola* (LESLEY und FROST, 1927). Das stimmt also nicht mit vorliegendem Fall. Ein anderer Umstand, der darauf hindeutet, dass eine Veränderung des Zeitunterschiedes zwischen Beginn der Prophase und Chromosomenteilung in diesem Fall nicht auf die Paarung und Kontraktion eingewirkt hat, ist der, dass alle P.M.Z. sich ähnlich verhalten, sowohl die verspäteten als die übrigen. Die »Precocity»-Theorie kann somit keine Erklärung dieses Falles liefern.

In einem anderen Zusammenhang hat DARLINGTON (1932) das Verhältnis zwischen Chromosomenkontraktion und Chiasmabildung berührt, das ja seiner Ansicht nach zu Metaphasepaarung führt. Im Kapitel »Evidence of how crossing over occurs» (S. 288), behandelt er die zuerst von BELLING (1931) ausgesprochene »torsion»-Hypothese. Gemäss dieser Hypothese verursacht die im späten Pachytän einsetzende Spiraldrehung, d. h. Kontraktion der Chromosomen, dass die Chromatiden reissen können. Sie vereinigen sich dann wieder in solcher Weise, dass ein Chromatid von neuer Zusammensetzung entstehen kann. D. h. »crossing over» und Chiasmabildung haben stattgefunden. Die Wiedervereinigung der Chromatiden geschieht ausserdem so, dass die Drehungsspannung herabgesetzt wird. Nach einer eingehenden Erörterung, über die ich hier nicht berichten kann, sondern für die ich auf sein Buch verweisen muss, gelangt DARLINGTON zu folgender Annahme (S. 292): »These observations indicate a common control of

chromosome contraction, of crossing over, and of chiasma formation in the spindle attachment, which may be supposed to institute the torsion that determines them all».

Auf Grund dieser Hypothese scheint mir etwa folgende Erklärung des vorliegenden Falles möglich zu sein: *Durch eine genetisch oder ev. von Aussenfaktoren bedingte abnorm starke Spiraldrehung der Chromosomen ist der »crossing-over»-Mechanismus in irgendeiner Weise gestört worden, und das Ergebnis sind ausgebliebene Metaphasepaarung und abnorm stark kontrahierte Chromosomen.*

SUMMARY.

1. The meiosis of two hybrids, representing different combinations of varieties, between *Triticum turgidum* ($n = 14$) and *Secale cereale* ($n = 7$) is described.

2. One, hybrid A, may have as many as 6_{II} and occasionally 1 or 1_{IV}. The highest association observed is $5_{II} + 1_{III}$, and the average number of bivalents is 1,6.

3. Some cases of unequal bivalents, ring-shaped univalents and probably double attachment chromatids indicate structural changes of chromosomes.

4. For various reasons, cytological and genetical, it is assumed that the chromosome pairing is probably exclusively autosyndetic.

5. A comparison between the pairing in triploid wheat × rye hybrids (with the genome constitution A B R) and the tetraploid (A B C R) shows that the highest number of bivalents, 6, is the same in both, and the frequency of pairing probably a little higher in the triploid. Consequently, the C-genome of *vulgare* wheat cannot be related to the rye-genome R, and it must be concluded that the *vulgare* wheat has not arisen by crosses between *Triticum dicoccum* and rye, as assumed by MEISTER.

6. The hybrid B is characterized by an abnormally great contraction of the chromosomes at meiosis: they have an almost spherical shape at first metaphase.

7. There is almost complete asyndesis (average number of bivalents 0,2).

8. In a number of P.M.C. the chromosomes do not separate at anaphase, but stick together. Usually, however, the cytokinesis follows, and only in a few cases a restitution nucleus is formed.

9. On the basis of the »torsion hypothesis» of crossing over, as

advanced by DARLINGTON (1932), an attempt has been made to find a relation between the abnormally great chromosome contraction and the asyndesis.

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THE EVOLUTIONARY SIGNIFICANCE OF AUTOPOLYPLOIDY

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I. INTRODUCTION.

ORIGINALLY the present work was initiated on account of some discussions concerning the species concept in the light of recent cyto-genetic results. In connection with these discussions, for which I am very much indebted to Professor G. TURESSON and Dr. O. TEDIN, the present writer undertook a detailed study of the properties of intraspecific chromosome races. I soon found it necessary to extend this work to related fields of research, dealing chiefly with experimental and natural autopolyploidy. The conclusions reached, which emphasize the evolutionary importance of autopolyploidy, are chiefly based on comparative studies of literature and only to a limited extent on my own experience.

For more than twenty years the phenomenon of heteroploidy and especially of polyploidy has been subject to intensive interest and research. In the first place this is due to the very frequent occurrence of polyploidy in the plant kingdom, at least fifty per cent and probably more of the Angiosperm species being polyploids. Though extremely remarkable *per se*, the problem of the multiple chromosome series became still more important and entered into a new phase when different workers succeeded in producing polyploid plants experimentally. Then the question naturally arose whether the natural polyploids had arisen in a similar way to that of the polyploids produced in experiments.

It was soon realized that polyploidy is of two different kinds, involving either reduplication of the same genome or summation of different genomes. In 1927 KIHARA and ONO coined the terms auto- and allopolyploidy for these two categories.

It is now perfectly clear that allopolyploidy has played an important rôle in the evolution of plant species, at least among Angiosperms. This has been demonstrated not only by the rather numerous and well-known instances of new artificial species, such as *Primula*

Kewensis, Nicotiana digluta, Aegilotricum and *Raphano-Brassica,* but still more strikingly by the experimental synthesis *de novo* of natural species from other species with lower chromosome numbers (*Phleum, Galeopsis*, cf. MÜNTZING, 1932 a).

With regard to the evolutionary importance of autopolyploidy there is a great diversity of opinion among the various workers.

As *Oenothera Lamarckiana* is a structural hybrid it is somewhat uncertain whether *Oenothera Lamarckiana gigas* should be regarded as an auto- or allotetraploid. It is generally regarded as an autotetraploid, however, and then as the very first autotetraploid observed in experimental cultures. On account of the new properties of *Oenothera gigas*, especially the new chromosome number, the striking morphological characters and the occurrence of a sterility barrier between *gigas* and *Lamarckiana*, DE VRIES regarded *Oenothera Lamarckiana gigas* as a new species produced by mutation (cf. DE VRIES, 1913). In his important paper of 1916, describing the experimental polyploids in *Solanum*, WINKLER criticizes DE VRIES' opinion concerning *Oenothera gigas* and states that *gigas* is not a new species but only a tetraploid form of *Oenothera Lamarckiana.* For WINKLER, the morphological differences between the diploid and tetraploid are too slight to be regarded as specifically different, and the sterility barrier, emphasized by DE VRIES, is not considered to be significant by WINKLER, owing to the very frequent occurrence of sterility in »pure» *Oenothera* species. — Nor does WINKLER regard his *Solanum* tetraploids as new species and is thus decidedly opposed to the view that chromosome doubling should be a factor in evolution. In a later paper, however, the same author (WINKLER, 1920, p. 168) suggests the hypothesis that »heterogenomatische Organismen» may arise from such as are »homogenomatisch».

On account of his thorough work with heteroploidy in moss species v. WETTSTEIN has reached rather definite conclusions with respect to the morphological and physiological effects and the evolutionary importance of auto- and allopolyploidy. As autopolyploid, in contrast to allopolyploid, moss strains, especially after repeated doubling, are more or less abnormal and cytologically unstable, v. WETTSTEIN (1927, 1928, 1932) considers autopolyploidy to be of little or no evolutionary significance. It is only for the breeding of new strains of cultivated plants that autopolyploidy may be of importance. In his paper of 1927 the author even considers that natural polyploidy in general is possible only by means of apomixis or pronounced vegetative propagation.

A similar, though less extreme, opinion is advanced by AFZELIUS

(1924), CLAUSEN (1926) and NAWASCHIN (1927). AFZELIUS (l. c. pp. 198—199) states that polyploid *species* cannot possibly arise only by multiplication of the same genome. Hybridization must be responsible for the qualitative differences existing between the polyploid species. CLAUSEN (l. c. p. 135) also considers autopolyploidy to be of little importance in evolution. No new combinations are formed in that way and autopolyploid products are not stable, but sooner or later revert to the diploid original type. NAWASCHIN, finally, (l. c. p. 205) points out that autotetraploidy (in contrast to triploidy) »keine grosse Rolle in der Formbildung spielt» as gigas types do not show any significant deviations from the diploid type and do not segregate in their progeny.

In contrast to the authors just mentioned, another group of geneticists are convinced that autopolyploidy is of fundamental importance for the evolution of plant species.

In 1919 BLAKESLEE and AVERY described a distinctly new race of *Datura stramonium*, which was found to be almost entirely, if not absolutely, sterile with other forms. BLAKESLEE stresses this physiological incompatibility between the mutant and the parent species from which it arose, and suggests that it should be regarded as a new species. Later on, when it was found that this mutant was tetraploid, BLAKESLEE (1921) raises the question as to whether such tetraploids occur in nature and are capable of giving rise to taxonomically new species. Despite the paucity of evidence at that time BLAKESLEE suggests that tetraploidy of the same kind as that found in *Datura* may have been one of the principal methods in the evolution of plants and says that its occurrence would furnish the barrier between a new species and its parental form, which DARWIN sought.

Several years later, JØRGENSEN (1928), working with *Solanum*, draws similar or even more advanced conclusions concerning the importance of autopolyploidy. JØRGENSEN (l. c. p. 200) points to the existence of many varieties and even species which must be autopolyploid. In contrast to BLAKESLEE, however, he does not consider autotetraploids as new species but as material from which such may differentiate. During this differentiation, which mainly should consist of structural changes, the quadrivalents characteristic of autotetraploids would disappear and be replaced by bivalents. — JØRGENSEN considers that the majority of polyploid species have in that way been differentiated from autopolyploids of pure species (l. c. p. 204) and emphasizes that such autopolyploids may easily arise by means of somatic doubling.

In his textbook of cytology, DARLINGTON (1932) agrees with

JØRGENSEN concerning the importance of structural changes as a means of transferring an original autopolyploidy to allopolyploidy (l. c. pp. 210—211) but seems to consider that autopolyploid species are very rare in nature and that such species, as a rule, are apomictic or characterized by vegetative propagation.

During their comprehensive studies of the genus *Crepis*, BABCOCK and his co-workers have reached some very definite conclusions as to the different evolutionary processes, which are at work in this genus. One of the most important of these processes is autopolyploidy. According to BABCOCK (1934), autotetraploid forms of existing species of *Crepis* are fairly common and a number of distinct *Crepis* species are known, which apparently arose through (auto-) tetraploidy. Further, BABCOCK and CAMERON (1934) state that there are two general processes by means of which new chromosome numbers have originated in *Crepis*, viz. by interspecific hybridization with amphidiploidy and by polyploidy (*i. e.* autopolyploidy).

Other workers who from their experience have reason to consider autopolyploidy as a factor in species formation are, e. g. SAX (1935, p. 114), FERNANDES (1934, p. 187) and LILIENFELD (1933, pp. 455—57).

It is evident from the instances cited above that opinions concerning the evolutionary importance of autopolyploidy are very divergent. This is not only a historical fact but is also characteristic of the present situation. On account of this uncertainty the present writer has made an attempt to furnish a new contribution to the discussion and to reach more definite conclusions, which are based on the evidence presented in the following pages.

II. INTRASPECIFIC CHROMOSOME RACES.

Most plant species seem to be characterized by one specific chromosome number, which is to be found in all individuals of each species. A number of species are known, however, which comprise different races, having different chromosome numbers. The number of such species is rapidly increasing.

In his paper on *Viola canina*, CLAUSEN (1931 a) has tabulated a number of species, comprising different chromosome races. Similar lists are to be found in DARLINGTON's cytology (DARLINGTON, 1932, pp. 211—212) and in the *Primula* paper of BRUUN (BRUUN, 1932, pp. 155—158). Besides an enumeration of species with oscillating chromosome number CLAUSEN's list contains 26 amphimictic and 7 apo-

mictic [1] species, comprising races with different chromosome numbers. One year later (1932) DARLINGTON reports 33 species as examples of polyploidy within the species, and in the same year BRUUN (l. c.) cites about the same number. Since 1932 many new cases of intraspecific chromosome variation have been described. In a recent paper by TISCHLER (1935) about 80 such species are briefly mentioned. Indeed, it is now difficult to avoid the suspicion that such races will be found in a very large number of plant species, if these are thoroughly investigated. Already now the number of species, showing intraspecific variation in chromosome number, may be estimated at one hundred at the lowest.

In order to get a sufficient basis for conclusions as to the average characteristics of intraspecific chromosome races, the present writer has studied and tabulated fifty-eight such cases, involving about seventy species (Table 1, pp. 270—277). This is not an exhaustive list of all cases hitherto known, but it contains a sufficiently large number of representative cases to allow the drawing of rather definite conclusions.

In the great majority of these cases we have to deal with *intraspecific polyploidy*, the different races being members of a typical multiple series. Only in a few cases, as in *Erophila verna* or *Scirpus palustris*, are the numbers more irregular, though constant in each race. Species with oscillating chromosome number, such as *Prunus laurocerasus* (MEURMAN, 1929 b), *Viola canina* (CLAUSEN, 1931 a) or *Poa alpina* (MÜNTZING, 1932 b) have not been included in the table.

In some cases, of course, it is difficult to decide where the species limits should be drawn, and consequently, whether we have to deal with intraspecific chromosome races or with closely related but separate species. Cases 43—58 belong to this more or less dubious category, whereas Cases 1—42 may be regarded as quite typical, in the sense that the different karyological types belong to one distinct morphological unit, which constitutes the species in question. As will be shown in the following pages the typical and the dubious cases have essentially the same properties and may thus be included in the same table.

A few remarks concerning the taxonomy of Cases 43—58 may, however, precede the detailed discussion. Several of these species are collective species, comprising different subspecies or varieties. This is true of *Erophila verna*, *Rumex pulcher*, *Polygonum aviculare*, *Betula*

[1] *Potentilla argentea*, placed by CLAUSEN in category C of his table, has been shown to be apomictic by the present writer and should therefore more correctly be included in category D (apomictic types).

alba and *Festuca elatior*. In other cases the species are now considered distinct, though closely related, but have earlier been described as units within one and the same species. Such cases are *Phleum nodosum—pratense*, *Viola stagnina—elatior*, *Viola biflora—crassa*, *Dactylis glomerata—Aschersoniana*, the *Eragrostis* species and *Empetrum nigrum—hermaphroditum*.

The situation in *Phleum* was cleared up by the cytological results of GREGOR and SANSOME (1930), who found that the *pratense* types corresponding to *Phleum nodosum* L. (cf. MÜNTZING, 1935) had 14 chromosomes, the other *pratense* types, corresponding to ordinary cultivated timothy, having $2n = 42$. *Viola stagnina* and *elatior* are more unlike but in the earlier editions of the Flora of Scandinavia by HARTMAN (1820—1879) these two types were not separated as distinct species. At any rate they are very closely related. The same holds true of *Viola biflora* and *crassa*. According to MIYAJI (1929—1930, p. 39) *V. crassa* was first described by MAKINO as a variety of *biflora* under the name of var. *crassifolia* but later the same author raised it to the rank of a separate species. *Dactylis Aschersoniana* was not described as a separate species until 1899 (GRAEBNER, cf. SAMUELSSON, 1923) and as late as 1929 TURESSON regards *Aschersoniana* as a shade ecotype of *glomerata*. Finally, the *Eragrostis* species were not distinguished until quite recently (cf. HAGERUP, 1931, p. 29) and *Empetrum hermaphroditum* was considered a variety of *nigrum* until HAGERUP (1927) discovered the difference in chromosome number. The same close relationship is characteristic of the remaining »dubious» cases (Nos. 48, 49, 50, 54 and 55), though I do not know for certain how long they have been regarded as specifically different. These cases, as well as the others, will be discussed in detail in the following pages.

The 58 cases in Table 1 all refer to amphimictic species or at least to species which have not been shown to be apomictic. Several apomictic species also comprise different chromosome races, which in many respects have the same properties as the races of amphimictic species. Reference to a number of such cases will be made below.

The frequent occurrence of intraspecific chromosome races is a remarkable phenomenon, which merits careful analysis. By means of the material presented in Table 1 I have tried to answer the following main questions:

1) Are the chromosome races morphologically different and, if so, are the differences qualitative or quantitative?

2) Is there any clear correlation between chromosome number and morphology?

3) Are the chromosome races ecologically identical or different?

4) Are the chromosome races separated by barriers of incompatibility and sterility, or are they quite fertile with each other?

5) How is fertility and cytological constancy in the polyploid chromosome races?

6) Are the polyploid chromosome races to be considered as auto- or as allopolyploid?

Unfortunately the data supplied in the different papers are rather incomplete, and often only the difference in chromosome number is stated. As far as possible, however, these six questions, which cover the most important characteristics of the chromosome races, will be answered in the following pages.

1. THE MORPHOLOGY OF INTRASPECIFIC CHROMOSOME RACES.

From Table 1 it is evident that *intraspecific chromosome races are practically always morphologically more or less different from each other.* In 10 of the 58 cases no data concerning morphology are given, but in all the remaining 48 cases differences occur. As the races belong to one and the same species it is *a priori* clear that the differences cannot be very striking and, indeed, quite often they are rather slight. However, not a single case is known, in which it has been demonstrated that the races are morphologically identical.

Concerning the nature of the morphological differences, these may roughly be considered to be either quantitative or qualitative. Sometimes it may be difficult to decide whether a difference should be regarded as quantitative or qualitative but in most cases there is no hesitation. In fact, *the great majority of the species consist of races that are quantitatively different.*

The 48 cases, in which morphological data are given, fall into the following categories: In 28 cases (24 of which are quite certain, 4 somewhat uncertain, cf. the summary below p. 280) the differences are only or almost only quantitative, in 5 cases both quantitative and qualitative, in one case only a qualitative difference is reported and in 14 cases differences are said to occur, but their nature is not reported.

It is obvious that intraspecific variation must generally be of a quantitative nature, since qualitative differences would probably raise the deviating type to the rank of a new species. Under such circumstances it might be suggested that the quantitative differences found to

TABLE 1. *The essential properties in 58 cases of intraspecific chromosome races.*

Case	Species	Morphology	Ecology	Incompatibility and sterility	Meiosis in the polyploid races
1	*Allium Schoenoprasum* L. 2 n = 16 and 32 TURESSON 1931 a, LEVAN 1931 and 1936	Quantitative differences, positive correlation between chromosome number and vigour	Different geographical distribution and other ecological differences	Partial incompatibility, F_1-hybrids partially sterile	A few IV in the tetraploid, III frequent in triploid hybrids
2	*Stellaria neglecta* WEIHE 2 n = 22 and 44 PETERSON 1935 (and unpublished results)	Quantitative differences, positive correlation	Different distribution and other ecological differences	Complete incompatibility	—
3	*Draba magellanica* LAM. 2 n = 24, 32 and 40 HEILBORN 1927	Quantitative and qualitative differences, probably positive correlation	Probably different distribution	—	—
4	*Phleum alpinum* L. 2 n = 14 and 28 Cf. MÜNTZING 1935 and H. NORDENSKIÖLD (unpublished data)	Differences occur but their nature has not been studied	Different distribution	Crosses between 2 n- and 4 n-races successful, but F_1 completely sterile	No multivalents in the tetraploid
5	*Rosa acicularis* LINDL. 2 n = 42 and 56 ERLANSON 1929	Differences occur but their nature has not been studied	Probably different distribution and other ecological differences	—	—
6	*Rosa subserrulata* RYDB. 2 n = 14 and 28 ERLANSON 1929	—	—	—	—
7	*Viola Kitaibeliana* ROEM. et SCHULT., sens. lat. 2 n = 14, 16, 24, 36 and 48 CLAUSEN 1927, 1929 and 1931 b	Quantitative differences but not straight line regression	—	Probably partial incompatibility, F_1-hybrids partially sterile	No multivalents
8	*Potentilla opaca* L. 2 n = 14 and 28 TISCHLER 1929	Differences present but their nature not studied	—	—	—
9	*Scirpus palustris* L. 2 n = 16 and 38 HÅKANSSON 1929 a	Quantitative differences, positive correlation	Probably different distribution	—	—

8	*Potentilla opaca* L. 2 n = 14 and 28 TISCHLER 1929	Differences present but their nature not studied	—	—	—
9	*Scirpus palustris* L. 2 n = 16 and 38 HÅKANSSON 1929 a	Quantitative differences, positive correlation	Probably different distribution	—	—
10	*Silene ciliata* POURR. 2 n = 24, 48 and 192 BLACKBURN 1928, 1930 and 1933	Differences present but their nature not closely studied	—	—	IV observed in the tetraploids, larger associations in the 16-ploid
11	*Salix aurita* L. 2 n = 38 and 76 HÅKANSSON 1929 b	—	Possibly different distribution	—	—
12	*Anemone* species *A. montana* HOFFE 2 n = 32 and 48 *A. nemorosa* L. 2 n = 32 and 39 MOFFETT 1932	—	—	—	—
13	*Nasturtium officinale* R. BR. 2 n = 32, 48 and 64 MANTON 1932, 1935	Quantitative differences, positive correlation	Different distribution and other ecological differences	Partial incompatibility, F_1-hybrids partially sterile	No multivalents
14	Several *Dianthus* species ANDERSSON-KOTTÖ and GAIRDNER 1931	—	—	—	—
15	*Biscutella laevigata* L. 2 n = 18 and 36 MANTON 1934 (and unpublished results)	—	Different distribution and other ecological differences	Triploid hybrids partially sterile	High frequency of IV in tetraploids and of III in triploid hybrids
16	*Narcissus bulbocodium* L. 2 n = 14, 28, 35 and 42 FERNANDES 1934	Quantitative differences but not straight line regression	Different distribution	—	—
17	9 *Galium* species Multiples of 11; 2 n ranging from 22—96 FAGERLIND 1934	Slight quantitative differences?	—	Incompatibility between different races of *G. Mollugo*	Low frequency of multivalents

Case	Species	Morphology	Ecology	Incompatibility and sterility	Meiosis in the polyploid races
18	*Portulacca oleracea* L. 2 n = 14 and 54 HAGERUP 1931	Quantitative differences, positive correlation	Grow together in one locality, otherwise not studied	—	—
19	*Vaccinium uliginosum* L. 2 n = 24 and 48 HAGERUP 1933	Quantitative differences, positive correlation	Different distribution	—	Occurrence of IV or marked secondary association
20	*Pentstemon azureus* BENTH. subsp. *parvulus* 2 n = 32 subsp. *typicus* and *angustissimus* 2 n = abt 48 CLAUSEN 1933	Quantitative differences, positive correlation	Different distribution	—	Multivalents in the hexaploid, IV in the tetraploid
21	*Vicia cracca* L. 2 n = 12, 14 and 28 SWESCHNIKOWA 1928 and 1929	Slight quantitative differences, positive correlation	Probably different distribution	Almost complete incompatibility between 14- and 28-chromosome races	—
22	*Aegilops triaristata* WILLD. 2 n = 28 and 42 SCHIEMANN 1929	Differences occur but their nature has not been studied	—	—	—
23	*Callitriche stagnalis* SCOP. 2 n = 10 and 20 JØRGENSEN 1925	Slight quantitative differences, positive correlation	—	—	—
24	*Festuca ovina* L. 2 n = 14, 28, 42, 70 LEVITSKY and KUZMINA 1927, STÄHLIN 1929	Both quantitative and qualitative differences, probably positive correlation	Different distribution and other ecological differences	—	—
25	*Festuca rubra* L. 2 n = 14, 42, 56, 70 LEVITSKY and KUZMINA 1929, STÄHLIN 1929	Both quantitative and qualitative differences, probably positive correlation	Different distribution and other ecological differences	—	—
26	*Tripsacum dactyloides* 2 n = 36 and 72 MANGELSDORF and REEVES 1931	Quantitative differences, positive correlation	Probably different distribution	—	Quadrivalents occur

25	*Festuca rubra* L. 2 n = 14, 42, 56, 70 LEVITSKY and KUZMINA 1929, STÄHLIN 1929	Both quantitative and qualitative differences, probably positive correlation	Different distribution and other ecological differences	—	—
26	*Tripsacum dactyloides* 2 n = 36 and 72 MANGELSDORF and REEVES 1931	Quantitative differences, positive correlation	Probably different distribution	—	Quadrivalents occur
27	*Tradescantia canaliculata* RAF., *occidentalis* (BRITTON) SMYTH and several other species 2 n and 4 n ANDERSON and DIEHL 1932, ANDERSON and WOODSON 1935	Differences occur but their nature not reported	Different distribution	F_1-hybrids highly sterile	High frequency of IV in the tetraploids and of III in triploid hybrids
28	*Cicuta virosa* 2 n = 22 and 44 MELDERIS 1930 (according to HÅKANSSON 1933)	—	Probably different distribution	—	—
29	*Astrantia* species 2 n = 14 and 28 HÅKANSSON 1933	Quantitative differences, positive correlation	—	—	—
30	*Pimpinella saxifraga* L. 2 n = 18 and 36 HÅKANSSON 1933	—	Possibly different distribution	—	Multivalents occur
31	*Aegilops crassa* BOISS. 2 n = 28 and 42 PERCIVAL 1927	Qualitative difference reported, otherwise not studied	Probably different distribution	—	—
32	Several *Ranunculus* species *R. acris* L. 2 n = 14 and 28 *R. repens* L., 2 n = 16 and 32 *R. auricomus* L. 2 n = 32 and 48 *R. lanuginosus* L. 2 n = 14 and 28 BRUUN 1932	Differences occur but their nature not reported	Different distribution	—	—

Case	Species	Morphology	Ecology	Incompatibility and sterility	Meiosis in the polyploid races
33	*Primula scotica* 2 n = 54 and 72 BRUUN 1930 and 1932	Differences occur but their nature not reported	Different distribution	—	—
34	*Caltha palustris* L. Different subspecies and varieties 2 n = 32, 56, 58 and 60 LANGLET 1932	Differences occur but their nature not reported	—	—	—
35	*Valeriana officinalis* L. 2 n = 14, 28 and 56 SENJANINOVA 1927	Differences occur but their nature not reported	Different distribution and other ecological differences	—	—
36	*Thalictrum simplex* L. 2 n = 56 and 70 KUHN 1928	—	Probably different distribution	—	—
37	*Opuntia polyacantha* HAW. 2 n = 44 and + 66 STOCKWELL 1935	Both quantitative and qualitative differences, negative correlation	Different distribution	—	—
38	*Iris aphylla* L. 2 n = 24 and 48 SIMONET 1934 c	—	Different distribution	—	—
39	*Iris Sintenesii* JANKA 2 n = 16 and 32 SIMONET 1934 c	Quantitative differences, positive correlation	—	—	—
40	*Plantago lanceolata* L. 2 n = 12, 24 and 96 MC CULLAGH 1934	—	—	—	—
41	Several *Crepis* species *C. occidentalis* NUTT. 2 n = 22 and 44 *C. gracilis* (EAT.) RYDB.	Differences occur but their nature not reported			

40	2 n = 12, 24 and 96 Mc Cullagh 1934	—	—	—	—
41	Several *Crepis* species *C. occidentalis* Nutt. 2 n = 22 and 44 *C. gracilis* (Eat.) Rydb. 2 n = 22 and 55 *C. acuminata* Nutt. 2 n = 33, 44? and 55? *C. barbigera* Leib. 2 n = 44 and 88? Hollingshead and Babcock 1930	Differences occur but their nature not reported	—	—	—
42	*Campanula rotundifolia* L. 2 n = 34 and 68 Böcher 1936	Quantitative differences, positive correlation	Different distribution	—	No multivalents(?)
43	*Erophila verna* E. Mey. 2 n = 14, 28, 30, 32, 36, 38, 52, 58 and 64 Winge 1926, 1933	Quantitative differences, positive correlation	—	Hybrids between different chromosome races have reduced fertility	—
44	*Phleum nodosum* L. — *pratense* L. 2 n = 14 and 42 Gregor and Sansomé 1930, Gregor 1931, Gregor and Horne 1935, Müntzing 1935	Quantitative differences, positive correlation	Ecological differences	Complete incompatibility or F_1-hybrids with unexpected chromosome numbers	No multivalents
45	*Viola stagnina* Kit. — *elatior* Fries 2 n = 20 and 40 Clausen 1927	Quantitative differences, positive correlation	Ecological differences	—	Quadrivalents occur
46	*Viola biflora* L. — *crassa* Makino 2 n = 12 and 48 Miyaji 1929—1930	Quantitative differences, positive correlation	Ecological differences	—	—

Case	Species	Morphology	Ecology	Incompatibility and sterility	Meiosis in the polyploid races
47	*Dactylis Aschersoniana* GRAEBN. — *glomerata* L. 2 n = 14 and 28 LEVAN 1930, MÜNTZING 1933a (and unpubl. results)	Quantitative differences, positive correlation	Different distribution and other ecological differences	F_1- hybrids completely male sterile but partially female fertile	High frequency of IV in the tetraploid and of III in triploid hybrids
48	*Dianthus sinensis* L. — *Seguieri* VILL. 2 n = 60 and 90 ROHWEDER 1934	Slight quantitative and qualitative (?) differences, probably positive correlation	Ecological differences	—	—
49	*Dianthus superbus* L. — *arenarius* L. 2 n = 30 and 60 ROHWEDER 1934	Both quantitative and qualitative differences, probably positive correlation	Ecological differences	—	—
50	*Chrysanthemum indicum* L. — *Shimotomaii* MAK. 2 n = 36 and 54 SHIMOTOMAI 1933	Quantitative differences, positive correlation	Different distribution and other ecological differences	Probably partial incompatibility	No multivalents
51	Collective species *Rumex pulcher* *R. pulcher* L. 2 n = 20 *R. dentatus* L. 2 n = 40 JARETZSKY 1928	Quantitative differences, positive correlation	—	—	Probably IV, at least marked secondary association
52	Collective species *Polygonum aviculare* L. *P. Bellardi* ALL. 2 n = 20 *P. monspeliense* THIÉBAUD 2 n = 40 *P. aviculare* L. 2 n = 40 JARETZSKY 1928	Differences occur but their nature not reported	—	—	—
53	*Eragrostis cambessediana* KUNTH. — *albida* HITCH. — *pallescens* HITCH. 2 n = 20, 40 and 80	Quantitative differences, positive correlation	Ecological differences	—	—

	P. aviculare L. 2 n = 40 JARETZSKY 1928				
53	*Eragrostis cambessediana* KUNTH. — *albida* HITCH. — *pallescens* HITCH. 2 n = 20, 40 and 80 HAGERUP 1931	Quantitative differences, positive correlation	Ecological differences	—	—
54	*Vallisneria spiralis* L. — *gigantea* GRAEBN. 2 n = 20 and 40 JØRGENSEN 1927	Quantitative differences, positive correlation	—	—	—
55	*Fothergilla monticola* — *major* 2 n = 48 and 72 ANDERSON and SAX 1935	Probably quantitative differences and positive correlation	—	—	—
56	Collective species *Betula alba* L. *B. verrucosa* EHRH. 2 n = 28 *B. pubescens* EHRH. 2 n = 56 HELMS and JØRGENSEN 1927	Differences occur but their nature not reported	—	—	—
57	*Empetrum nigrum* L. — *hermaphroditum* (LGE) HAGERUP 2 n = 26 and 52 HAGERUP 1927	Quantitative differences, positive correlation	Different distribution	—	Probably IV, at least marked secondary association
58	Collective species *Festuca elatior* L. *F. pratensis* HUDS. 2 n = 14 *F. arundinacea* SCHREB. 2 n = 42 Cf. PETO 1933, JENKIN 1933	Quantitative differences, positive correlation	Ecological differences	Partial incompatibility, F_1-hybrids partially sterile	No multivalents

exist between most races should be of the same kind as those present between any biotypes of the species, irrespective of chromosome number. This is not the case, however, as on an average *there is a marked positive correlation between chromosome number and gigas characters* in the material studied. The races having the higher chromosome numbers tend to be vegetatively more robust and have often thicker leaves and larger seeds than the races with lower chromosome number.

Among the 28 cases, in which the differences were quantitative, positive correlation between chromosome number and quantitative characters was found to occur in 26 cases, whereas in 2 cases there was no clear correlation. The positive correlation generally prevailing may be exemplified as follows:

The tetraploid gigas race of *Allium Schoenoprasum* (Case 1) is larger than the diploid in all vegetative parts and has also larger flowers and seeds (LEVAN, 1936)[1]. The tetraploid *Stellaria neglecta* var. *grandiflora* (Case 2) has exactly the same properties. The *Scirpus* races (Case 9) are more similar, but the race with the higher chromosome number has larger capsules. The same holds true of Case 23 (*Callitriche*). In *Nasturtium* (Case 13) the tetraploid race has bigger fruits, seeds and flowers than the diploid. In Cases 18, 19 and 42 (*Portulacca*, *Vaccinium* and *Campanula*) the polyploid races, according to the descriptions and reproductions of HAGERUP and BÖCHER, are very pronounced gigas types as compared with the diploids. — In *Pentstemon azureus* (Case 20) the small corolla and anthers of subsp. *parvulus* ($2n = 32$) are very characteristic and are even used as key characters to distinguish this race from the subsp. *typicus* and *angustissimus*, which have considerably larger corolla and anthers and also a higher chromosome number ($2n = \pm 48$).

Case 21 (*Vicia cracca*) is a more doubtful example, but according to SWESCHNIKOWA (l. c.) the tetraploid race ($2n = 28$) has »breitere Blättchen in Zusammenhang mit den grösseren Zellen und eine grössere Zahl von Samen in den Bohnen» than the corresponding diploid ($2n = 14$). In *Tripsacum* (Case 26) the tetraploid type seems to be coarser and to have broader leaves than the diploid, and as to *Astrantia* (Case 29) the tetraploid is said to be »grosswüchsig». In *Iris Sintenesii* (Case 39) the races are again distinguished by quantitative differences. The tetraploid is taller and has larger flowers than the diploid.

[1] According to LEVAN (l. c.) this species also includes less vigorous presumably allotetraploid biotypes. As these are of unknown origin and less thoroughly studied than the gigas type they will not be further considered in the present paper.

The remaining cases to be mentioned in this connection all belong to the latter part of Table 1, which (as mentioned above p. 267) refers to such races as are morphologically rather different. Nevertheless we have here the same kind of correlation as in the previous cases.

In *Erophila verna* (Case 43) the size of the leaves is roughly proportional to the chromosome number. In *Phleum* (Case 44), *Viola* (Cases 45—46), *Dactylis* (Case 47), *Vallisneria* (Case 54) and *Festuca* (Case 58) the races with the higher chromosome number exhibit very marked gigas characters as compared to the corresponding diploids. For details I must refer the reader to the respective papers cited in Table 1. I will only mention that in *Dactylis*, according to measurements made last summer, the average plant weight in the tetraploid *glomerata* was found to be 544 gr. (four biotypes), the corresponding value in the diploid *Aschersoniana* being 179 gr. (ten biotypes).

In a number of other cases, belonging to the same category, the gigas characters are not always very striking. In *Chrysanthemum* (Case 50), however, the type with the higher chromosome number has larger flower heads, more robust stem and thicker leaves than the other race. A similar situation is met with in *Rumex* (Case 51) and in *Empetrum* (Case 57). The tetraploid *Rumex* race is more vigorous, with bigger fruits and fruit dents than the diploid race (l. c. p. 380). Finally, the tetraploid *Empetrum hermaphroditum* is again described as being more robust than the diploid *nigrum*. The plant is taller and the leaves larger (l. c. p. 12).

Cases 3 (*Draba*), 24, 25 (*Festuca*) and 49 (*Dianthus*) represent races (or closely related species), distinguished by both qualitative and quantitative characters. With respect to the latter character the same positive correlation as before is probably present. In *Draba magellanica* there is possibly a certain relation between chromosome number and stature. In *Festuca ovina*, TURESSON (1930) has found a marked correlation between chromosome number and vigour in some viviparous strains. A similar correlation between sexual strains of the same species has been observed by JENKIN (1933, p. 256). Concerning *Dianthus*, the correlation between morphology and chromosome number has not been much investigated, but *D. arenarius* seems to have larger buds than *superbus* (ROHWEDER, 1934, p. 340).

It remains to consider three cases in which the regression between gigas characters and chromosome number is not straight line or even negative. The single negative case (Table 1, Case 37) is represented by an *Opuntia* species, which occurs in two races having $2n = 44$ and

± 66 respectively. The 66-chromosome race, which has a northern distribution, is described as much smaller and having smoother pads and fewer spines than its southern relatives with 2n = 44.

In *Viola Kitaibeliana* (Case 7), CLAUSEN (1931 b, p. 230) describes three races having n = 7, 18 and 24 respectively. The first race is a tiny type from Caucasia, the second one (also from Caucasia) is stout and erect and in its vegetative parts distinct from the preceding race. The third race, however, obtained from the Island of Jersey in the English Channel, was found to be the smallest of the three races and even more tiny than *Kitaibeliana* n = 7.

A similar situation is met with in *Narcissus bulbocodium*, in which species four different chromosomal races (2n, 4n, 5n and 6n) have been described by FERNANDES (cf. Table 1, Case 16). There is an excellent positive correlation between chromosome number and vigour when the first three races are compared, but the 6n-type is quite small. Just as in *Viola Kitaibeliana*, the race having the very highest chromosome number is inferior in vegetative vigour. This exceptional behaviour will be further discussed below (p. 287). But first it may be convenient to summarize the morphology of the intraspecific chromosome races in the following way.

1) *Quantitative or almost exclusively quantitative differences, positive correlation.*
Cases: 1, 2, 9, 13, 18, 19, 20, 21(?), 23, 26, 29, 39, 42, 43, 44, 45, 46, 47, 48(?), 50, 51, 53(?), 54, 55(?), 57, 58.
Total: *26 cases* (*45 per cent*).

2) *Quantitative differences but not straight line regression.*
Cases: 7, 16.
Total: *2 cases* (*3 per cent*).

3) *Both quantitative and qualitative differences, probably positive correlation.*
Cases: 3, 24, 25, 49.
Total: *4 cases* (*7 per cent*).

4) *Qualitative difference reported, otherwise not studied.*
Case: 31.
Total: *1 case* (*2 per cent*).

5) *Both quantitative and qualitative differences, negative correlation.*
Case: 37.
Total: *1 case* (*2 per cent*).

6) *Differences are present but their nature is not reported.*
Cases: 4, 5, 8, 10, 17?, 22, 27, 32, 33, 34, 35, 41, 52, 56.
Total: *14 cases* (*24 per cent*).

7) *Morphological characters not studied.*
Cases: 6, 11, 12, 14, 15, 28, 30, 36, 38, 40.
Total: *10 cases* (*17 per cent*).

It is quite evident from the above figures and examples that, on an average, the cases of intraspecific chromosome races are characterized by a very marked positive correlation between chromosome number and gigas characters. In experimentally produced autopolyploids and in some allopolyploids the well-known and typical gigas characters are undoubtedly caused by the increased chromosome number. It may consequently be concluded that *the gigas characters of polyploid chromosome races are caused by the higher chromosome numbers.* The correlation found is not merely the expression of a parallelism but surely demonstrates a causal connection between the two phenomena.

2. COMPARISON BETWEEN THE MORPHOLOGY OF EXPERIMENTAL AUTOTETRAPLOIDS AND POLYPLOID CHROMOSOME RACES.

In order to substantiate the conclusion concerning a causal connection between high chromosome number and gigas characters it may be convenient to make a short comparison between the morphological characters of experimental autopolyploids and those found in the polyploid chromosome races. From the elementary text-books of genetics we know that autotetraploids are more robust in all vegetative and floral parts but not necessarily taller than their corresponding diploids. The stem and the leaves are generally thicker, the leaves larger. The buds and the flowers, including the reproductive organs and the pollen grains, have also greater dimensions. The same holds true concerning the size and weight of the seeds. The tetraploid is mainly a magnified edition of the diploid. Though certain morphological differences may occur, which are not strictly quantitative (e. g. a slightly altered leaf shape), the general appearance of the tetraploid differs only in quantity from that of the diploid.

The most well-known examples of autotetraploids are those of *Solanum lycopersicum* and *nigrum* (WINKLER, 1916; JØRGENSEN, 1928; LINDSTROM and KOOS, 1931; KOSTOFF and KENDALL, 1934, and other workers), several moss species (cf. v. WETTSTEIN, 1924 b), *Datura stramonium* (BELLING and BLAKESLEE, 1924; BLAKESLEE, 1928) and *Pri-*

mula sinensis (KEEBLE, 1912; cf. SANSOME and PHILP, 1932). As already mentioned, the origin and constitution of *Oenothera Lamarckiana gigas* have been subject to some controversy, but probably this type may be considered as an autotetraploid. In such a case it is the very first autotetraploid observed and studied (cf. LEHMANN, 1922; RENNER, 1933). As is well-known it presents the same typical gigas characters as were found later in other autotetraploids.

In order to get a more concrete survey of the morphological characteristics of autotetraploids in higher plants I have compared eight different characters in the species mentioned above (except the moss species) and gathered additional data from the following papers: UFER (1927) concerning *Cleome spinosa* and *gigantea*, HONING (1928) concerning *Canna aureo-vittata*, BABCOCK and NAVASHIN (1930), NAWASCHIN (1927) and NAVASHIN (1931) concerning *Crepis*, and finally NISHIYAMA (1934) concerning *Avena*. The most characteristic properties were found to be the following:

1) *The stem of the tetraploid is thicker and stouter than that of the diploid.* — This is true of *Solanum lycopersicum, S. nigrum, Primula sinensis, Datura stramonium, Oenothera Lamarckiana, Cleome spinosa* and probably also *Canna aureo-vittata.* In *Cleome* the stem of the gigas type is angular and about $^1/_3$ thicker than that of the diploid.

2) *The tetraploid is taller than the diploid.* — As the tetraploids are robust they should often be taller than the diploid. This, however, is definitely stated only for *Solanum lycopersicum* and *nigrum*, according to WINKLER and JØRGENSEN (l. c.). The tetraploid tomatoes studied by KOSTOFF and KENDALL were of about the same size as the diploids or slightly taller after a longer period of growth (l. c. p. 24).

3) *The tetraploid has larger leaves than the diploid.* — Larger leaves characterize at least the tetraploids of *Solanum lycopersicum* and *nigrum* and also *Datura.* In *Cleome*, UFER did not find any significant difference between gigas and normal.

4) *The tetraploid has thicker leaves than the diploid.* — This has been observed in the two *Solanum* species and in *Cleome.* — In the latter species the bracts too are thicker in the gigas type.

5) *The leaves are relatively shorter and broader in the tetraploid.* — The tetraploids very often have a lower value of the leaf index than the diploids. This has been found in the *Solanum* species, in *Oenothera, Cleome spinosa* and *Canna aureo-vittata.* Even the cotyledons may

show this characteristic difference, as observed by JØRGENSEN in *Solanum lycopersicum.*

6) *The leaves are of a darker green in the tetraploid.* — A characteristic difference in the green colour was observed in the *Solanum* species by WINKLER, JØRGENSEN and by KOSTOFF and KENDALL, the tetraploids being darker green. The same thing is reported for *Oenothera Lamarckiana gigas* (DE VRIES, 1906) and for *Cleome spinosa.*

7) *The flowers and floral parts are bigger in the tetraploid.* — The difference in flower size between diploid and tetraploid is often striking and almost always present. As a rule the size of the reproductive organs is correlated with that of the petals. Larger flowers have been observed in *Oenothera*, *Solanum lycopersicum* and *nigrum*, *Cleome*, *Primula sinensis*, *Datura stramonium*, *Crepis capillaris* and *tectorum*, *Canna aureo-vittata* and in an autotetraploid derivative from the cross *Avena barbata* × *strigosa* (NISHIYAMA, 1934). Correlated with the bigger flowers is often an increased size of the flower buds, as observed in the *Solanum* species and in *Cleome*. The increase in flower size may often be considerable. LINDSTROM and KOOS (1931) found that the flowers of tetraploid tomato were 40 % bigger than in the diploid.

In this connection it may be remembered that many ornamental plants are in all probability autopolyploids. As such they show a marked correlation between chromosome number and flower size. Such is the situation e. g. in *Narcissus* (cf. NAGAO, 1933; FERNANDES, 1934). Some other striking examples of the same thing have been given by SIMONET (1932) concerning *Iris* and *Iberis.*

8) *The seeds are bigger in the tetraploid.* — On account of the partial sterility characteristic of autotetraploids (vide below) the fruits (if they normally contain many seeds) are often smaller than in the diploid. The seeds, however, are generally larger in the tetraploid than in the diploid. This holds true of the following cases: *Solanum nigrum*, *Cleome spinosa* and *gigantea*, *Crepis* species (NAWASCHIN, 1927), *Avena*, probably also *Datura.* — In the two *Cleome* species the relative weight of the seeds in tetraploid and diploid was found to be 513 : 334 and 362 : 270 respectively.

When the morphology of the experimental autotetraploids is compared with that of the polyploid chromosome races *a striking similarity is obvious.* In the numerous cases, in which positive correlation between chromosome number and gigas characters was found, the differences between the races are of exactly the same kind as those recorded in

the experimental material. The races with the higher chromosome numbers are very often more robust, with thicker stems, larger leaves, flowers and seeds. This similarity is best reflected by Table 2, which may be regarded as a morphological summary. At the head of this table Figures 1—8 denote the eight different characteristics of experimental autotetraploids (cf. pp. 282—283). The upper part of the table shows the distribution of those characters among the different cases of experimental autotetraploidy discussed. The lower part of the table shows the frequency and distribution of the same gigas characters among those wild polyploid chromosome races which showed positive correlation between chromosome number and gigas characters. Only the four somewhat dubious cases mentioned earlier (p. 269) have been omitted. The + signs in the table indicate the presence of the gigas character in question. The — signs, in most cases, indicate that the character has not been studied or reported. In a minority of cases it represents the observed absence of the gigas character. No attempt has been made to distinguish between the two latter categories. This uncertainty, however, probably affects the reported cases of experimental autopolyploids to about the same degree as the chromosome races.

One conclusion from the table is at once quite evident. *Polyploid chromosome races very frequently exhibit the same kind of gigas characters as experimental autotetraploids and often to about the same degree.* In some cases the gigantism is probably only partial but the evidence is yet too meagre to allow further distinctions and conclusions.

Especially through the work of v. WETTSTEIN and his school it has been demonstrated that the morphological alterations in experimental autopolyploids are ultimately due to alterations in cell size. As is well-known there is a positive correlation, though not strict proportionality, between chromosome number and cell volume. Consequently, in experimental autotetraploids cell size is greater than in the corresponding diploids. This has indeed been found to be the case in practically all the experimental tetraploids discussed, and is definitely stated for the following species: *Solanum lycopersicum* and *nigrum*, *Cleome spinosa* and *gigantea*, *Primula sinensis*, *Oenothera Lamarckiana*, *Datura stramonium*, *Crepis tectorum* and *capillaris*.

Fortunately, cell size has also been observed in some polyploid chromosome races and was found to be greater than in the corresponding diploids. With reference to Table 1 the following cases were found to behave in that way: 1, 3, 9, 10, 13, 16, 19, 21, 23, 39, 43, 44, 47 and 57. In these cases either the size of the nuclei and cells or the size of pollen

TABLE 2. *Comparison between the morphology of experimental autotetraploids and polyploid chromosome races.*

	Species	Morphological character number							
		1	2	3	4	5	6	7	8
Experimental autotetraploids	*Cleome spinosa* and *C. gigantea*	+	−	−	+	+	+	+	+
	Canna aureo-viltata	+	−	−	−	+	−	+	−
	Solanum lycopersicum	+	+	+	+	+	+	+	−
	Solanum nigrum	+	+	+	+	+	+	+	+
	Primula sinensis	+	−	−	−	−	−	+	−
	Oenothera Lamarckiana	+	−	−	−	+	+	+	−
	Datura stramonium	+	−	+	−	−	−	+	−
	Crepis tectorum	»giant characteristics»						+	+(?)
	Crepis capillaris	»small although very fleshy»						+	+(?)
	Avena (derivatives from the cross *barbata* × *strigosa*)	»gigas plants»						+	+
Polyploid intraspecific chromosome races	Case 1 (Table 1)	+	+	+	+	−	−	+	+
	» 2	+	+	+	+	−	−	+	+
	» 9	−	−	−	−	−	−	−	+
	» 13	−	−	−	−	−	−	+	+
	» 18	+	−	+	−	+	−	+	−
	» 19	+	+	+	−	−	−	+	−
	» 20	−	−	−	−	−	−	+	−
	» 23	−	−	−	−	−	+		+
	» 26	+	+	+	−	−	−	−	−
	» 29	+	+	−	−	−	−	−	−
	» 39	−	+	−	−	−	−	+	−
	» 42	+	+	+	−	−	−	+	−
	» 43	−	−	+	−	−	−	−	+
	» 44	+	+	+	−	−	−	+	+
	» 45	»all the parts are larger»							
	» 46	the giant characteristics not specified							
	» 47	+	+	+	+	−	+	−	+
	» 50	+	−	−	+	−	−	+	−
	» 51	+?	+?	+?	−	−	−	−	+
	» 54	+	+	+	+	+	−	+	−
	» 57	+	+	+	−	+	−	−	−
	» 58	+	+	+	+	−	+	−	−

mother cells and pollen grains have been measured and found to be correlated with the chromosome number. Consequently it is perfectly clear that *the morphological homology between experimental autopolyploids and polyploid chromosome races is due to an increased cell size.* The greater size of the cells is in both cases caused by the increased chromosome number.

When comparing the morphology of the chromosome races with that of experimental material we have hitherto exclusively referred to experimental autotetraploids. The numerous autotriploids described are also as a rule vigorous and have gigas characters. These, however, are generally less pronounced than in the tetraploids. On the other hand haploids, having smaller cells, are known to be miniature forms as compared to the normal diploids (cf. HOLLINGSHEAD, 1930; LINDSTROM and KOOS, 1931; BLEIER, 1933).

Thus, the morphology is very strongly correlated with the chromosome number. It has been found, however, that there is an optimum for chromosome increase beyond which the individuals become less vigorous if they are viable at all. The position of this optimum seems to be rather different in different organisms. In some species even the tetraploids are not very successful. According to SANSOME and PHILP (1932, p. 180), the autotetraploid *Primula obconica* does not show any increased vigour as compared to the diploid of the same species. The autotetraploid *Crepis capillaris* (BABCOCK and NAVASHIN, 1930) is even inferior in vigour as compared to the diploid.

This correlation between chromosome number and vigour has been specially studied by v. WETTSTEIN. According to this author (v. WETTSTEIN, 1927), the limit of autopolyploid chromosome increase in the moss species is always reached by the tetravalent races, which have four times the normal chromosome number. In the higher plants this would correspond to an octoploid condition. Some autooctoploids have really been produced in maize (RANDOLPH, 1932) and were found to be dwarf plants with poor viability in contrast to the vigorous autotetraploids.

From my own experience I may mention the genus *Dactylis*, in which *D. glomerata* may be regarded as an autotetraploid of *D. Aschersoniana* (MÜNTZING, 1933 a, and unpublished results). Pentaploid derivatives from the cross *glomerata* × *Aschersoniana* are on an average even more vigorous than *glomerata* but an octoploid individual ($2n = 56$) was a dwarf plant, which soon died in spite of all efforts to keep it alive.

YAMAMOTO (1935) describes an autohexaploid *Rumex acetosa*, having poor viability but gigas flowers. Further cases which may be of a similar nature are described by LEVAN in *Allium* (LEVAN, 1936, p. 44) and by CHEESMAN (1932) concerning *Musa*. In *Allium* the chromosome numbers in F_2 of the cross between diploid and tetraploid *A. Schoenoprasum* ($2n = 16$ and 32 respectively) ranged from 16 to 45. The plant having $2n = 45$ was quite poor in viability. In *Musa* the vigour of plants having 22, 33, 44, and about 55, 75 and 90 chromosomes could be compared. The 90- and 75-chromosome plants were dwarfs, the 55-plant somewhat better, the 44- and 33-chromosome plants very vigorous and larger than the normal diploids with 22 chromosomes. Though it is somewhat doubtful whether this series may be regarded as autopolyploid, it clearly demonstrates the existence of an optimum for chromosome increase.

In the wild plants such an optimum has been observed by STÄHLIN (1929) to be present in *Poa* and *Festuca*. In these genera, vigour generally increases from diploidy to hexaploidy. This is correlated with an increased size of the cells. Hexaploidy, however, seems to represent the optimum, since most octoploid species in these genera are smaller in size than the hexaploids or even the tetraploids.

As regards the polyploid chromosome races (Table 1), many of them are tetraploid, others represent higher multiples. It may be suggested that in those cases in which the regression between chromosome and gigas characters is not straight line (Cases 7 and 16) or negative (Case 37) this deviation from the rule may be due to the fact that the races in question have surpassed the optimum for chromosome increase.

In *Viola Kitaibeliana* (Case 7) the race with $n = 18$ was vigorous, as compared to that having $n = 7$, but the type with $n = 24$ was quite small. These three types may be regarded as approximately diploid, hexaploid and octoploid respectively (CLAUSEN, 1931 b, p. 299). Thus, it is quite possible, though not proved, that the octoploid type is beyond the chromosome optimum. This is still more probable in the case of *Narcissus bulbocodium* (Case 16). As mentioned earlier there is a positive correlation between chromosome and vigour among the 2n, 4n and 5n races of this species but the 6n type is smaller than the 2n type. Finally, it should be mentioned that both the *Opuntia* races showing negative correlation (Table 1, Case 37) have rather high chromosome numbers ($2n = 44$ and ± 66). It is possible that the optimum is situated between 44 and 66.

3. THE ECOLOGY OF INTRASPECIFIC CHROMOSOME RACES.

The data concerning the ecology of the chromosome races studied are summarized in Table 1. In 20 cases no data are given in the papers cited, in the remaining 38 cases geographical distribution or other ecological characters are mentioned.

A study of the table at once reveals the fact that *the chromosome races are probably always ecologically different.* This is demonstrated either by different geographical distribution or by other ecological characters. As a basis for further discussion the data from Table 1 may be summarized under the following headings:

1) *Different geographical distribution in combination with other ecological differences.*
Cases: 1, 2, 13, 15, 24, 25, 35, 47, 50.
Total: *9 cases* (*16 per cent*).

2) *Different ecology.*
Cases: 44, 45?, 46, 48, 49, 53, 58.
Total: *7 cases* (*12 per cent*).

3) *Different geographical distribution.*
Cases: 4, 16, 19, 20, 27, 32, 33, 37, 38, 42, 57.
Total: *11 cases* (*19 per cent*).

4) *Probably different geographical distribution.*
Cases: 3, 9, 21, 26, 28, 31, 36.
Total: *7 cases* (*12 per cent*).

5) *Probably different geographical distribution and other ecological differences.*
Case: 5.
Total: *1 case* (*2 per cent*).

6) *Possibly different geographical distribution.*
Cases: 11, 30.
Total: *2 cases* (*3 per cent*).

7) *Grow together in one locality, otherwise not studied.*
Case: 18.
Total: *1 case* (*2 per cent*).

8) *Ecology not studied or reported.*
Cases: 6, 7, 8, 10, 12, 14, 17, 22, 23, 29, 34, 39, 40, 41, 43, 51, 52, 54, 55, 56.
Total: *20 cases* (*34 per cent*).

Though the data reported are often rather incomplete it is evidently quite typical for the races to have different geographical distributions. That is certainly the fact in twenty cases (Categories 1 + 3) and with probability in ten additional cases. Thus, *in 30 of the 38 cases, in which data are given, the races have definitely or probably different geographical distributions.*

With regard to the eight remaining cases, seven are known to be ecologically different and to occupy different habitats, whereas in the eighth case it is not known whether the different races are ecologically different or not.

In order to verify the ecological summary presented above, it will be necessary to describe a couple of cases in detail. Starting with category 1, different distribution in combination with other ecological differences, we have first to consider Case 1, *Allium Schoenoprasum*. The tetraploid gigas type was discovered by TURESSON (1931 a) in East-Altai, where it grows in abundant quantities at a relatively low sea-level, especially along the shores of Lake Teletskoje. Another type from East-Altai was subalpine and found to be diploid (LEVAN, 1936, p. 9) like most other types of this species. Besides this difference in distribution, the diploids and the tetraploid gigas type differ also in another ecological respect, the rate of growth. The tetraploid is slow-growing and reaches its definite size much later than the diploids (LEVAN, l. c. p. 48).

The species representing Case 2, *Stellaria neglecta*, comprises a tetraploid variety *grandiflora*, which (verbal information by Dr. D. PETERSON) has a Mediterranean distribution in contrast to the typical diploid variety, which is more northern. Further, the diploid *neglecta* grows in forests, the tetraploid seems to be an adventitious plant.

In Case 13, *Nasturtium officinale*, the tetraploid race has a more northern distribution than the diploid (MANTON, 1935, fig. 1). Combined with this difference in distribution there is a marked difference in the growth rate, the tetraploids being more slow-growing and hardy than the diploids. Moreover, the diploids have a tendency to behave as annuals, the tetraploids (and triploids) as perennials.

In another species, *Biscutella laevigata* (Case 15), studied by the same author, the tetraploids inhabit nearly the whole area occupied by the Alpine Ice Sheet during the Glacial Period. The diploids, on the contrary, seem to be relics and occupy another area, which is more favoured climatically. Further, the tetraploids, in contrast to the diploids, have a capacity to develop adventitious buds on their roots.

In the genus *Dactylis* (Case 47) the very closely related species *glomerata* (tetraploid) and *Aschersoniana* (diploid) have a different geographical distribution, the area of *glomerata* being extended farther to the north than that of *Aschersoniana*. Further, *Aschersoniana* is a typical forest plant which, at least in South Sweden, grows only in the shady beech woods; *glomerata* is usually found growing in meadows and at ditch edges but seldom in the woods.

A similar state of things is met with in *Chrysanthemum* (Case 50). The very closely related species *Shimotomaii* and *indicum* have separate distribution areas. This is evidently due to a true ecological difference, for *Shimotomaii* is a sea-shore plant, whereas *indicum* grows in the fields and mountains but seldom along the coast.

The remaining cases (Nos. 24, 25 and 35), included in Category 1 (cf. p. 288), are not so adequately known as the cases just described. Nevertheless the information at hand justifies the conclusion that the races in question are ecologically different and have a different distribution. Both the *Festuca* species, *rubra* and *ovina*, contain several different chromosome races. According to JENKIN (1933, p. 255 and p. 260), these polyploid races have probably contributed more to the extension and distribution of the genus than to effective competition in those areas where the diploids existed. Consequently, the function of polyploidy in *Festuca*, as in other genera, appears to be the production of types which are capable of extending the ecological range.

Finally, *Valeriana officinalis* L. (sensu lato), representing Case 35 (Table 1), evidently behaves in a rather similar way. According to the brief remarks of SENJANINOVA (1927, p. 676), the different chromosome races ($2n = 14$, 28 and 56) are not only morphologically different but also have different distribution and ecology.

The second category (p. 288) includes seven cases in which the races are known to have a different ecology, their distribution, however, being unknown or coinciding. The most interesting example of this kind is Case 53, the *Eragrostis* species studied by HAGERUP (1931). The diploid type is fragile and adapted to favourable, very moist, habitats, on the shores of small lakes. The tetraploid type is found at less moist habitats and is perennial in contrast to the diploid, which is annual. The third type, which is octoploid, grows in the sand dunes and is very markedly xerophile and also perennial.

The other six cases in this category are also quite clearly differentiated in an ecological respect. I will only mention, with regard to Case 46, that *Viola crassa* is xerophile and alpine, whereas *biflora* is a

hygrophile lowland type (cf. MIYAJI, 1929—1930, p. 39). *Festuca elatior* (Case 58) includes the hexaploid *F. arundinacea* and the diploid *F. pratensis*. The former is a sea-shore plant, the latter generally growing in meadows. Finally, *Dianthus arenarius* (Case 49) is strictly adapted to arenacious fields, whereas *superbus* generally grows in meadows or moors.

The survey of the ecological differences between chromosome races may be concluded by a few examples from Category 3, which contains those cases which have different geographical distributions and consequently, in all probability, different ecological properties.

The diploid *Phleum alpinum* (Case 4) grows in Switzerland, the tetraploid types studied were obtained from Scotland and Northern Scandinavia. Still more striking are Cases 19 and 42, *Vaccinium uliginosum* and *Campanula rotundifolia*. Both these species contain arctic diploid races, growing in Greenland, and tetraploid races with a more southern distribution. — All the other cases, belonging to this category, behave in a similar way and are known to have decidedly different distribution areas. To avoid needless repetition I must refer the reader to the papers cited in Table 1. The same reference may be made as regards Categories 4—7, summarized on p. 288. They contain cases which no doubt in principle behave like Categories 1—3 but have not been so thoroughly investigated.

Table 1 and the instances given above, however, suffice to demonstrate with absolute certainty that *chromosome races are ecologically different*. Only in one case (No. 18) is the possibility open that the races have the same ecological properties. Upon closer examination even this case will probably reveal differences. In fact, *not a single case is known in which it has been demonstrated that intraspecific chromosome races are ecologically identical*. In view of the data reported in Table 1 it does not either seem likely that such cases will ever be found.

These facts harmonize very well with the conclusions previously arrived at by NAVASHIN (1929) and HAGERUP (1927, 1931, 1933).

Especially on account of his experience from arctic as well as desert plants, HAGERUP (l. c.) very strongly emphasizes the fact that the races studied by him and cited in the present paper are ecologically different. This is thought to be due to the difference in chromosome number because »with polyploidy there may follow a change in the ecological and plant-geographical value of the plant» (HAGERUP, 1933, p. 127). — NAVASHIN holds the same opinion on account of his ex-

perimental results in *Crepis* (NAVASHIN, 1929). Triploid individuals of *Crepis capillaris* were found to be much more slowly growing than diploid plants. NAVASHIN emphasizes that this might be ecologically valuable if it occurs in nature. The rate of development might play a decided rôle in the invasion of an area by a new polyploid form. In this connection reference is made to the polyploid species *Crepis biennis*, which has a different geographical distribution from that of the related diploid species *C. capillaris*.

The observations of NAVASHIN will be discussed in the next chapter, together with other experimental evidence, which may explain the remarkable fact that chromosome races are ecologically different. Before that, however, another aspect of the problem may be briefly considered.

Different authors, when making comparative counts of chromosome numbers in genera or families, have noticed that species with high chromosome numbers seem to have a more northern distribution than related species with lower numbers. This correlation between chromosome number and geographical distribution has recently been investigated by TISCHLER (1935), studying the flora of Schleswig-Holstein. TISCHLER found that 60 per cent of the species in this province, having a northern distribution, are polyploid, whereas the corresponding figure of the species characterized by a southern distribution was only 27. This result coincides with the fact that 55 per cent of the species of Iceland were found to be polyploid but only 31 per cent of the species of Sicily.

A similar condition might be expected to prevail with regard to the intraspecific chromosome races, tabulated in the present paper. Unfortunately rather few of them are known to be distinctly different as regards a southern or northern distribution. In the following cases (cf. Table 1), however, the race with the higher chromosome number is more northern than the race with the lower number: 4, 13, 20, 26, 27, 37, 57. In addition to these seven cases, in which the difference in north-south distribution is quite definite, two somewhat doubtful cases, Nos. 9 and 21, may be added.

If a northern distribution means increased hardiness, which is probable, it should be mentioned that in Case 46 the race with the higher chromosome number is alpine and xerophile in contrast to the diploid lowland race. A similar situation is met with in Case 15 (*Biscutella*). The diploid race is found only in habitats which are favoured climatically. The tetraploid race is mainly alpine.

On the other hand three cases are known (Nos. 2, 19 and 42) in

which, on the contrary, the diploid race is more northern. Specially striking examples are the diploid arctic races of *Vaccinium* and *Campanula.*

In spite of these marked exceptions the present material, though not large enough to be decisive, supports the theory that polyploids are on an average more hardy than diploids and hence better adapted to a northern or alpine distribution.

4. THE PHYSIOLOGICAL CONSEQUENCES OF CHROMOSOME DOUBLING.

The most striking properties of experimental autopolyploids are no doubt the morphological gigas characters. These have attracted attention to such an extent that the physiological side of the problem has been somewhat neglected. — The morphological alterations are known to result mainly from the increased cell size. *A priori* it is probable that a change in cell size will also have *physiological* conseqences. Indeed, a number of observations have been made which show that this is the case.

The investigations of NAVASHIN (1929) have already been mentioned. The triploid individuals of *Crepis capillaris* were much more slow-growing than the diploids and most of them started to bloom about a month later than the diploid sister plants. Quite similar observations have been made concerning a number of other autopolyploids. The classical case of *Oenothera Lamarckiana gigas* also presents this feature. DE VRIES (1906) mentions that *gigas* has a greater tendency to be biennial than *Lamarckiana* and thinks that this is in some way correlated with a difference in the chemical activity. The strongly biennial character of *Oenothera Lamarckiana gigas* is also emphasized by GATES (1913, 1915) who considers the slower growth of *gigas* to be correlated with the increased ratio of volume to surface in the cells. GATES (1915) also mentions that the flowers of *gigas* are more susceptible to frost than those of diploid *Lamarckiana.* HERIBERT NILSSON (1920) has also noted the slower growth of *Oenothera gigas* and finds that the retarded growth is even characteristic of the pollen tubes. Tetraploid gigas types are known also in other *Oenothera* species than *Lamarckiana.* STOMPS (1925) has studied an *O. biennis gigas* which also seems to be more slow-growing than diploid *biennis* (»une des plantes fleurissant seulement dans la seconde année . . . était notre *O. biennis gigas*», l. c. p. 238).

Other autopolyploid Angiosperms, showing a decreased rate of

development, are the tetraploid races of *Solanum lycopersicum* (LESLEY and LESLEY, 1930; KOSTOFF and KENDALL, 1934), *Cleome spinosa* (UFER, 1927), *Canna aureo-vittata* (HONING, 1928), *Datura stramonium* (BLAKESLEE, verbal information) and *Primula sinensis* (KEEBLE, 1912). LESLEY and LESLEY (l. c.) noted that their tetraploid apparently grew more slowly than the diploid. They also found that tetraploid pollen mother cells in a diploid plant were always in a less advanced stage of maturation than adjacent diploid pollen mother cells. In the same way tetraploid islands in otherwise diploid root tips had a lowered rate of division. In this connection it should also be observed that JØRGENSEN (1928, p. 157) found the seeds of tetraploid tomato to be 3—5 days slower in germination than diploid seeds of the same species.

KOSTOFF and KENDALL (1934) emphasize that the vegetation period of the tetraploid tomato plants is prolonged. On an average the tetraploids began to flower not less than 45 days later than the diploid plants. The growth curves of the tetraploid and diploid are also quite different (l. c. p. 23, Table 1). In *Cleome spinosa*, UFER (l. c. p. 4) has tabulated the time of flowering in the normal race and the gigas type and finds that the gigas plants are considerably slower. The same thing is again met with in *Canna*. HONING (l. c. p. 5) reports that tetraploid individuals of *C. aureo-vittata* have noticeably slow growth and late flowering.

Besides the *Crepis* case first mentioned, some triploids, too, show a retardation in the rate of development. COLLINS (1933) reports that triploid varieties of *Ananas* mature more slowly than diploids. Finally, HEILBORN (1935) has observed that triploid apple varieties are slower than diploids in after-ripening and hence are superior with regard to durability and keeping quality.

All the cases mentioned seem to demonstrate that the effect of autopolyploidy is always a retardation of the growth rate. One case, however, has been reported which seems to be an exception to this rule. KOSTOFF and KENDALL (1931) found that an autoteraploid individual of *Petunia violacea* grew more rapidly than its diploid sister plants and began to flower about 8 days before them. As in this case only one single tetraploid individual was available, the difference observed may not be significant.

In several of the cases mentioned above the slower rate of development has been assumed to be due to a decreased rate of cell division. An analysis of polyploid moss races has furnished definite evidence to show that autopolyploidy has a marked effect on the rapidity of cell

division. v. WETTSTEIN (1924 a) remarks that an altered rate of cell division is characteristic of the experimental gigas races among the moss species. He also considers (v. WETTSTEIN, 1924 b) that the lower production of sporogones in *bivalens* races than in *univalens* races is partly due to a lower rate of cell division, hence production of female flowers, and partly to a slower mobility of the bivalent sperms.

The rate of cell division in moss races has been subject to a special investigation by DÖRRIES-RÜGER (1929), working with *Physcomitrium piriforme* and *Funaria hygrometrica*. This author got a somewhat surprising result, inasmuch as the bivalent races of the two species showed an *increase* in the rate of cell division in comparison with the univalent races. But a further increase of the chromosome number had the opposite effect. Trivalent and tetravalent races of *Physcomitrium* were progressively slower than the bivalent race. The figures found were the following: $0{,}53 \pm 0{,}02$ (*univalens*), $0{,}64 \pm 0{,}03$ (*bivalens*), $0{,}59 \pm 0{,}03$ (*trivalens*) and $0{,}50 \pm 0{,}03$ (*tetravalens*). In the other species, *Funaria hygrometrica*, the *univalens* race had the value $1{,}05 \pm 0{,}04$, the *bivalens* race $1{,}28 \pm 0{,}07$. — These experiments demonstrate a marked correlation between chromosome number and rate of cell division, but the regression is not straight line. If the optimum of the *bivalens* races is surpassed, we get the decrease in the rate of cell division, which was found to be typical of the higher plants.

Considering that the *univalens* races correspond to the gametophyte generation of the higher plants, it would be very interesting to know the behaviour of haploids among the Angiosperms. Unfortunately, practically nothing is known or reported concerning the rate of development in haploids, and until more data have accumulated we must therefore leave the question open.

A number of physiological consequences of chromosome doubling other than changed rate of cell division have been observed in the mosses as well as in other plants. — v. WETTSTEIN (1924 b, p. 199) remarks that there are considerable differences between *univalens* and *bivalens* races with respect to metabolism in general and with respect to the reaction against different ion-concentrations. — BECKER (1931) has studied the relation between chromosome number and osmotic pressure in moss species and finds that in the homogenomatic series of *Funaria hygrometrica* and *Physcomitrium piriforme* the osmotic pressure is inversely proportional to the chromosome number and therefore to the cell size. For the last mentioned species the pressure (in atmospheres) was found

to decrease continuously from $12{,}151 \pm 0{,}158$ (*univalens*) to $9{,}759 \pm 0{,}116$ (*tetravalens*).

HEILBRONN (1928) has studied the morphology and physiology of diploid and autotetraploid *Polypodium aureum*. He found (l. c. p. 843) that the production of starch was much more intensive in the tetraploid than in the diploid, the value obtained in the former being almost twice as high as that of the latter. — In a later paper (HEILBRONN, 1935) the same author reports that haploid and diploid protallia of the same fern species react differently to high temperature and to chloral hydrate. Further, experimental mutations could be obtained in the diploid but not in the haploid.

Turning to the higher plants, SANSOME and ZILVA (1933) have examined diploid and autotetraploid tomatoes for their vitamin C content. All the tetraploid strains were found to be about twice as active as the diploids. These results strengthen the evidence, obtained by CRANE and ZILVA (1931), that also in the case of apples there is a connection between the vitamin C content and the number of chromosomes.

In *Avena*, NISHIYAMA (1934) has observed that there is a positive correlation between chromosome number and resistance to cold, the diploid types being most susceptible, the tetraploids and especially the hexaploids being more resistant. This correlation also seems to hold true for a certain diploid segregation product from the cross *Avena barbata* × *strigosa*, and its autotetraploid derivative, the latter being decidedly more hardy than the former. This indicates that quantitative chromosome differences rather than specific genes are responsible for the different degrees of resistance observed.

KOSTOFF and AXAMITNAJA (1935 b) have made a chemical analysis of tetraploid tomato and *Petunia*, compared with the corresponding diploids. In *Petunia*, the principal chemical compounds of the tetraploid were, generally speaking, preserved and similar to the proportions found in the diploids. In the tomato the results were quite different. The tetraploids were found to contain more water and less cellulose and ashes than the diploids. Further, the tetraploids contained more nitrogen and proteins than the diploids. Other differences were found, too (l. c. p. 296). The different behaviour of the *Petunia* and tomato tetraploids is thought to be due to the fact that the *Petunia* tetraploid in contrast to the tomato tetraploid showed a proportional increase of all organs and elements. Be that as it may, the results at any rate demonstrate that *purely quantitative chromosome changes may have considerable chemical and thus physiological consequences.* In another

paper (KOSTOFF and AXAMITNAJA, 1935 a) the same authors describe the chemical analysis of certain *Nicotiana* amphidiploids and their corresponding F_1 hybrids. These have the same relations to each other as autotetraploids have to the corresponding diploids and may therefore be mentioned in this connection. The authors state that from a biochemical point of view the amphidiploids represent a quite new system, even when compared with the F_1 hybrids.

The instances hitherto cited, concerning the physiological consequences of chromosome doubling, have all been taken from plants, since polyploidy is very rare among animals. A few apomictic animal species, however, are known which include polyploid races. In one important physiological respect, these races behave just like plant species, the rate of development being obviously correlated with the chromosome number.

In *Artemia salina*, diploid, tetraploid and octoploid biotypes occur (cf. ARTOM, 1928; GROSS, 1932). From the arguments and observations made by these authors it is perfectly clear that in this species we have to deal with autopolyploidy in combination with apomixis. The polyploid races have larger cells and show a number of gigas characters as compared to the diploids. But in addition to these morphological effects physiological differences are also evident. ARTOM (l. c.) writes as follows: »En raison de ses caractères somatiques et biologiques, du développement accéléré de ses différentes parties, en raison même de la différence qui existe entre les éléments circulant dans l'hémolymphe, l'*Artemia salina* tétraploïde peut être considérée aujourd'hui comme un organisme qui, au point de vue morphologique et physiologique, n'a rien de commun avec l'*Artemia* diploïde».

GROSS (1932) reports that when the salt concentration of the culture medium is altered, diploid animals show another type of variability than octoploids. Consequently, *diploids and octoploids have different reaction norms*. This behaviour is quite comparable to the different reactions of haploid and diploid protallia in *Polypodium aureum*, as reported by HEILBRONN (1935, cf. above p. 296). Still more striking, however, is the fact that the octoploid individuals, just like the tetraploid tomatoes discussed above (p. 294), have a slower development and another type of growth curve than the diploids. This is evident from the following statement by GROSS (l. c.): »Was die Unterschiede in der absoluten Körperlänge bei diploiden und oktoploiden Tieren betrifft, so sind die oktoploiden Tiere kurz nach Erlangung der Geschlechtsreife kaum grösser als die diploiden in gleichem Stadium, jedoch scheint es

uns, dass die ersteren mit dem Alter stärker wachsen und eine ansehnlichere Grösse erreichen als die diploiden». The author further stresses this physiological difference in the following words: »Die Häufung mehrerer Genome in einem Ei bewirkt offensichtliche entwicklungsphysiologische Verschiebungen, die in ihrer Kompliziertheit weit über die älteren Anschauungen über die Kern-Plasma-Relation hinausgehen».

Also in another animal, the moth *Solenobia triquetrella*, similar physiological differences occur. According to SEILER (1927), this species comprises a diploid sexual as well as a tetraploid parthenogenetic race. Culture experiments with these races revealed a marked difference in the rate of development, the larvae and pupae of the tetraploid race being much slower than those of the diploid race (l. c. p. 432). Triploid F_1 individuals between the two races could also be obtained, and these were in fact observed to be intermediate in the rate of development.

From these observations in two animal species, combined with the numerous examples from autopolyploid plants cited above, it is perfectly clear that *the negative correlation between chromosome number and rate of development is a universal phenomenon almost without any exceptions.* As suggested by several of the authors cited, this retarded growth must be connected with the greater cell size which is quite regularly found in autopolyploid individuals.

Conclusion. — The experience hitherto accumulated concerning the physiological consequences of chromosome doubling may be summarized as follows: Purely quantitative alterations of the number of genomes influence not only the morphology but to a rather high degree also the physiology of the altered individuals. These react in a new way both with the normal environment and to changes of the normal environmental conditions. Most typical and universal is the altered growth rate, the types with the higher chromosome numbers generally being more slow in development. But also other important physiological properties, such as assimilation energy and winter-hardiness, may be greatly influenced by autopolyploidy. Chemical analyses have in certain cases revealed considerable differences between diploids and autopolyploids, and it has also been demonstrated that the concentration of certain vitamins may be altered. It is probable that many or all of these changes ultimately depend on a change in cell size. This may also cause a difference in the osmotic pressure as demonstrated in the mosses. Consequently, *autopolyploids have generally new physiological properties, new reaction norms.*

5. COMPARISON BETWEEN THE PHYSIOLOGICAL PROPERTIES OF CHROMOSOME RACES AND EXPERIMENTAL AUTOPOLYPLOIDS.

The main conclusion concerning the ecology of intraspecific chromosome races was that they are generally ecologically different. This is demonstrated by various ecological characteristics or by different geographical distributions. We have not yet discussed the question whether the chromosome races should be regarded as auto- or as allopolyploid. However, in any case *it is obvious that there must be a connection between the two phenomena: the ecological differentiation of intraspecific chromosome races and the physiological differences observed to arise as a consequence of experimental chromosome doubling.*

This connection becomes still more clear when the following facts are considered: The most striking physiological feature of experimental autopolyploids was found to be the change in growth rate. Now, in some cases the polyploid chromosome races present exactly this typical property. The polyploid apomictic types in *Artemia* and *Solenobia* have just been discussed. Turning to the plants we find that the tetraploid giant race of *Allium Schoenoprasum* is more slow-growing and needs a longer time to reach its full vegetative development than diploid types of the same species (LEVAN, 1936, p. 48). The same thing is met with in *Nasturtium* (MANTON, 1935). Among the diploid, triploid and tetraploid races described, there is positive correlation between low chromosome number, rapidity of growth and early production of flowers. The tetraploid race has a longer vegetative period and may be as much as 14 days later in flowering than the diploids. The triploid race was found to be intermediate (l. c. p. 142).

In *Nasturtium* it was also found (l. c. p. 151) that the diploids have a marked tendency to behave as annuals, whereas the polyploids are perennials. — The correlation between chromosome number and the kind of life form will be considered in a special chapter of the present paper. With reference to *Nasturtium* I will only mention already now that, according to SHARP (1934, p. 342), the autotetraploid maize plants, produced by RANDOLPH, are perennial, in contradistinction to ordinary diploid maize, which is annual.

When discussing the ecological differences between chromosome races, it was often mentioned that one race was more hardy than the other, as demonstrated by a northern or alpine distribution (cf. above p. 292). As a rule the type with the higher chromosome number was found to be the hardier. This harmonizes very well with the experi-

mental results of NISHIYAMA (1934) concerning the frost resistance of various *Avena* types (cf. above p. 296).

TISCHLER (1935) mentions that a certain category of sea-shore plants are almost exclusively polyploid and considers that these species would not be able to grow at such extreme habitats, if they were not represented by polyploid biotypes. Since the osmotic pressure is known to be influenced by polyploidy (BECKER, 1931; cf. above p. 295) it might be interesting to make a comparative study of the osmotic conditions and the chromosome number of such sea-shore plants. At any rate it is highly probable that the osmotic pressure is an important ecological factor, just as the other physical and chemical differences, which are known to result from chromosome doubling.

In the genus *Dianthus*, ROHWEDER (1934) has made some very interesting observations, based on culture experiments, regarding the relation between ecology and polyploidy. His results are especially interesting, since some *Dianthus* species include different chromosome races or are very closely related (cf. Table 1). ROHWEDER finds that all diploid *Dianthus* species are quite specialized and sensitive. They have poor adaptability and cannot stand lime and nitrogen. The diploid species also seem to have poor viability and to be dying out. They are difficult to cultivate. The tetraploid species are very much superior to their diploid relatives as regards resistance to lime and nitrogen and could be successfully cultivated under any conditions. The hexaploid species, finally, »gedeihen wie Unkraut» and are even easier to cultivate than the tetraploid species. They are to a marked degree »boden- und frostbeständig».

The instances cited may suffice to show that there are very close connections between polyploidy and changed ecological properties. Under such circumstances the ecological differences between intraspecific chromosome races are also quite comprehensible. Finally, it is evident that the natural chromosome races are not only morphologically but also physiologically quite similar to experimental autopolyploids.

6. THE RESULT OF CROSSES BETWEEN INTRASPECIFIC CHROMOSOME RACES.

In the intraspecific chromosome races we have the somewhat peculiar situation that races, which may be morphologically very similar, differ in chromosome number just as much as distinct species. Under these circumstances it may be difficult to estimate the taxonomical value of such races. — As the criterion of incompatibility and sterility

has been widely used both by taxonomists and geneticists in order to estimate taxonomic and genotypic relationship, it might be valuable to consider how intraspecific chromosome races behave in this respect.

Unfortunately, crossing experiments of this kind have been undertaken only to a very limited degree. Of the 58 cases reported in Table 1 only 14 have been subject to such experiments. The results obtained in these 14 cases, however, demonstrate that *the chromosome races are generally separated from each other by barriers of incompatibility and sterility*.

It may be worth while considering incompatibility and sterility separately. Both phenomena occur when chromosome races are crossed with each other. The cross may fail entirely or succeed with more or less difficulty and the F_1 hybrids, eventually obtained, may show different degrees and types of sterility.

Incompatibility of different degrees has been reported for the following nine cases (cf. Table 1): 1, 2, 7?, 13, 17?, 21, 44, 50, 58.

In Case 1 (*Allium Schoenoprasum*) the cross failed entirely in the direction 2n $\times$ 4n but gave positive result when the tetraploid was used as mother. However, even in this direction, 4n $\times$ 2n, the result was rather meagre. From 189 pollinated flowers as many as 150 seeds were obtained, but these were of bad quality and had poor germination. Altogether not more than 32 F_1 seedlings were obtained (l. c. p. 19). — In *Stellaria neglecta* (Case 2) crosses between tetraploid and diploid fail altogether, no germinable seeds being obtained in either direction.

Concerning the races of *Viola Kitaibeliana* (Case 7), nothing is stated as to incompatibility. In *Viola*, F_1 hybrids may generally be obtained rather easily, irrespective of chromosome number. As will be shown below (Table 5, p. 332), however, crosses between races with the same chromosome number even in *Viola* give better results than crosses between types with different numbers. Consequently there is some indirect evidence of incompatibility concerning crosses between the races of *Viola Kitaibeliana*.

In Case 13 (*Nasturtium*) there is direct evidence of incompatibility between diploid and tetraploid. The combination 4n $\times$ 2n gave fruits readily, but most of the fruits contained only shrunken and non-viable seeds. — As to Case 17 (*Galium*), FAGERLIND (1934) briefly mentions that different races of *Galium Mollugo* are incompatible with each other, as indicated by preliminary crossing experiments. — In *Vicia cracca* (Case 21) the same conditions are again met with. Out of 44 crosses

between races with 14 and 28 chromosomes only 2 grains were received (from the combination 2n × 4n).

According to GREGOR and SANSOME (1930, p. 376) and GREGOR (1931, p. 207), crosses between *Phleum nodosum* (2n) and *pratense* (6n) failed completely, and hybrids could not be obtained in spite of repeated efforts. Thus, in this case (No. 44) there is a very marked incompatibility barrier between the two races. This barrier, however, may not be absolute. The present writer (MÜNTZING, 1935) has studied derivatives from spontaneous hybrids between *nodosum* and *pratense*, and recently Miss H. NORDENSKIÖLD (unpublished results), working with the same material, has succeeded in obtaining artificial F_1 hybrids by using a male sterile *nodosum* type as the female parent. The F_1 hybrids obtained in this way, however, had 35 or 49 chromosomes instead of the expected number 28. — At any rate there is a very marked barrier of incompatibility between these two *Phleum* types.

In the last cases to be mentioned (Nos. 50 and 58) incompatibility is again evident but less extreme than in *Phleum*. The two closely related *Chrysanthemum* species, *Shimotomaii* and *indicum* (Case 50), may be successfully crossed, but SHIMOTOMAI (1933) reports that only 5 hybrid plants were obtained from 12 pollinated flower-heads. This relatively poor result is probably due to the difference in chromosome number (cf. below, p. 329). — *Festuca arundinacea* and *pratensis* (Case 58) have been successfully crossed by JENKIN (1933). In the direction *pratensis* ♀ × *arundinacea* ♂ 34 hybrid plants were obtained from 235 emasculated flowers, and a similar result was obtained in the reciprocal cross. A rather high percentage of apparently good caryopses were formed but these had relatively poor germability.

If F_1 hybrids are successfully produced, these hybrids will generally be partially sterile to different degrees. In rare cases they may be absolutely sterile. In the following ten cases (cf. Table 1) crosses between different intraspecific chromosome races have been reported to result in more or less sterile F_1 individuals: 1, 4, 7, 13, 15, 27, 43, 44, 47, 58.

In *Allium* (Case 1), the triploid F_1 plants showed a relatively good though markedly decreased fertility. In the parent races more than 90 per cent of the pollen was good, the corresponding value in F_1 being 75 per cent. The seed production after open pollination was found to be 3,5 seeds per flower in the diploid, 4,5 in the tetraploid and only 0,7 in the triploid (LEVAN, 1936, p. 24). Consequently, the seed production in the hybrid was less than 20 per cent of that in the parent races.

The F_1 hybrid between diploid and tetraploid *Phleum alpinum* (Case 4) seems to be completely sterile and a similar situation is met with in *Tradescantia* (Case 27). Crosses between diploid and tetraploid races of *Tradescantia canaliculata* and *occidentalis* gave sterile or almost sterile F_1 hybrids (ANDERSON and WOODSON, 1935, pp. 35—37).

In Case 7 (*Viola Kitaibeliana*), the F_1 hybrids of two different intraspecific combinations, 24×7 and 18×7, have proved to be partially sterile.

The wild triploid *Nasturtium* race (Case 13), which is homologous to artificial triploids, obtained from the cross $4n \times 2n$, is also partially sterile to a very marked degree. In spite of this sterility it may be able to survive, thanks to vegetative propagation (MANTON, 1935). According to a paper read by the same author at the International Botanical Congress in Amsterdam 1935, the triploid hybrids, obtained from crosses between tetraploid and diploid *Biscutella laevigata* (Case 15), are also partially sterile.

It remains to consider the F_1 fertility in Cases 43, 44, 47 and 58, which represent somewhat more distantly related races (cf. p. 267). Concerning *Erophila verna* (Case 43) it is known that hybrids between different chromosomal types have a more or less inferior fertility. The exceptional *Phleum* hybrids (Case 44), obtained by H. NORDENSKIÖLD and mentioned above, have relatively good fertility both on the male and female side, and the same is true of the F_1 hybrids between *Festuca pratensis* and *arundinacea*, as Dr. NILSSON-LEISSNER has kindly informed me. The *Dactylis* hybrid, finally, (Case 47) is completely male sterile but partially female sterile. A low percentage of seeds may be obtained after pollination with pollen from both the diploid and especially from the tetraploid parent type.

In the preceding chapters the morphological and physiological similarity between intraspecific chromosome races and experimental autopolyploids has been demonstrated. This similarity is also valid with regard to incompatibility and sterility. It is a striking fact that autotetraploids among the higher plants are generally more or less incompatible with the diploid original forms. In *Datura*, for example, crosses between 4n and 2n strains fail in the one direction ($2n \times 4n$), whereas the reciprocal cross gives a low proportion of viable seeds, from which triploids may be obtained (BELLING and BLAKESLEE, 1922). JØRGENSEN (1928) obtained the same result in crosses between tetraploid and diploid tomato. The few seeds produced were poorly developed and germinated with difficulty. LESLEY and LESLEY (1930), also working with tomato, had a similar experience.

Tetraploid × diploid set fruit fairly readily, but nearly all the seeds in these fruits were abortive. A few were of normal size, and two of them germinated. No viable seed was obtained from the reciprocal cross. LINDSTROM and HUMPHREY (1933) have also tried the same crosses both with *Solanum lycopersicum*, *pimpinellifolium* and the F_1 hybrid between these species. Their results were completely negative. Crosses between diploids and tetraploids always failed in both directions. No viable triploid seeds could be produced.

In *Campanula persicifolia* seed production is also low in crosses between 4n and 2n strains (GAIRDNER and DARLINGTON, according to WATKINS, 1932, p. 142). The same story is again met with in *Primula sinensis*. Hybrids between tetraploid and diploid strains of this species have only been obtained a few times, and the cross succeeds only with extreme difficulty (cf. DARLINGTON, 1931). — Finally, STOMPS (1925) reports that crosses between diploid and tetraploid *Oenothera biennis* give a very poor result. The germability of the seeds is poor and from 18 different crosses a total of only 36 seeds, capable of germination, were obtained.

These instances suffice to demonstrate the *complete similarity between chromosome races and experimental autopolyploids as regards incompatibility*. In both categories incompatibility may in some cases be absolute, in other cases less extreme, and in both categories different results are often obtained in reciprocal crosses. The causes of this incompatibility will be discussed below (p. 326).

Finally, if crosses between tetraploids and diploids really result in F_1 hybrids, these triploid individuals are partially sterile. This holds true both for experimental autotriploids and for triploid hybrids between chromosome races. As is well-known, this partial sterility must be ascribed to the fact that a high proportion of the gametes, from purely numerical reasons, will receive unbalanced and lethal chromosome complements.

7. ARE THE INTRASPECIFIC CHROMOSOME RACES AUTO- OR ALLOPOLYPLOID?

In order to elucidate the question whether the polyploid chromosome races are allo- or autopolyploid, the meiotic behaviour is of special interest. In experimental autopolyploids, having more than two homologous chromosomes of each kind, the formation of multiple associations is very characteristic. As is well-known, the maximum number of chromosomes in these associations corresponds to the number of

genomes present in the plant. In typical allopolyploids, on the contrary, only pairs of chromosomes are homologous, and consequently only bivalents are formed at meiosis. In short, the presence of multivalents indicates autopolyploidy, the absence of multivalents allopolyploidy. — In the chromosome races studied the following conditions were met with (cf. Table 1):

1) *The presence of multivalents indicates autopolyploidy.*
Cases: 1, 10, 15, 17, 19, 20, 26, 27, 30, 45, 47, 51?, 57?.
Total: *13 cases* (*22 per cent*).

2) *Meiosis not studied, but chromosome morphology indicates autopolyploidy.*
Cases: 39, 54.
Total: *2 cases* (*3 per cent*).

3) *No multivalents, but from other reasons probably autopolyploidy.*
Cases: 13, 50, 56.
Total: *3 cases* (*5 per cent*).

4) *The absence of multivalents indicates allopolyploidy.*
Cases: 4, 7?, 42?, 44, 58?.
Total: *5 cases* (*9 per cent*).

5) *Meiosis not studied.*
Cases: 2, 3, 5, 6, 8, 9, 11, 12, 14, 16, 18, 21, 22, 23?, 24, 25, 28, 29, 31, 32, 33, 34, 35, 36, 37, 38, 40, 41, 43?, 46, 48, 49, 52, 53, 55.
Total: *35 cases* (*60 per cent*).

From these data it is evident that next to Category 5, which represents those cases in which meiosis has not been studied at all, Category 1 is most typical. In the cases falling under this heading the polyploid races show multivalents at meiosis, whereas the diploid races have only bivalents. This indicates complete or partial autopolyploidy.

In the tetraploid gigas type of *Allium Schoenoprasum* (Case 1), there are from 1—4, mostly 2, quadrivalents at meiosis. In triploid hybrids, obtained by crossing tetraploid and diploid, there was a high frequency of trivalents. On an average there were 1,3 univalents per cell, which corresponds to 6,7 trivalents. Consequently, as the basic number is 8, about 84 per cent of the chromosomes occur as trivalents in the triploid, whereas in the tetraploid about 25 per cent are united to quadrivalents.

In tetraploid races of *Silene ciliata* (Case 10), the presence of about 4 quadrivalents at meiosis was observed. As the basic number in this

genus is 12, this means that about 33 per cent of the chromosomes were members of quadrivalents. In the 16-ploid race the configurations at meiosis could not be analysed in detail, but multivalents were observed, sometimes consisting of a rather large number of chromosomes. The inference, that the polyploid races in this species are autopolyploid, is supported by the fact that in the diploid two chromosomes have satellites, in the tetraploid four.

Concerning Case 15 (*Biscutella*), quadrivalents are frequent in the tetraploid, just as trivalents in triploid F_1 hybrids, produced by artificial crosses between the 2n and 4n races. However, the exact proportion of multivalents in this species has not yet been recorded. — Also in polyploid *Galium* races (Case 17) multivalents have been observed to occur, but their frequency seems to be low. In the tetraploid races of *Vaccinium* and *Empetrum*, studied by HAGERUP (Cases 19 and 57), the chromosomes at meiosis are said to be paired, which in these cases evidently signifies a high frequency of quadrivalents or at least a marked degree of secondary association. — Similar conditions seem to occur in *Rumex pulcher* (Case 51). JARETZSKY (1928, p. 380) mentions that the number of units at diakineses varied between 14 and 18, though the number should be 20, if only bivalents were present. — In *Pentstemon azureus* (Case 20), the races known are either tetraploid or hexaploid. The hexaploid subsp. *typicus* shows multivalents of unknown size and frequency, and in the tetraploid subsp. *parvulus* two quadrivalents occur almost regularly. — Further, quadrivalents in unknown frequency have been reported to be present in the tetraploid races of *Tripsacum dactyloides* (Case 26) and *Pimpinella saxifraga* (Case 30).

In *Tradescantia* (Case 27), both tetraploid races and species are reported to be autotetraploid ($2n = 24$), having a high frequency of quadrivalents at meiosis. In *T. reflexa* there was an average frequency of about 3,4 quadrivalents, which corresponds to 57 per cent of the chromosomes. In a triploid *Tradescantia bracteata*, KING (1933) observed an average of 5,4 trivalents per cell. Consequently, in this triploid not less than 90 per cent of the chromosomes were united to trivalents.

Case 45 (*Viola stagnina-elatior*) is less thoroughly known. In the tetraploid *elatior*, however, quadrivalents evidently occur. In CLAUSEN's paper (1927), Fig. 20 represents a first metaphase, in which about fourteen units can be counted, six of very large to medium size, and eight small. The configuration in this cell probably represents $6_{IV} + 8_{II}$.

In *Dactylis* (Case 47), finally, the frequencies of multivalents in 3n, 4n and 5n forms have been compared (MÜNTZING, unpublished data).

In triploid hybrids between *Aschersoniana* and *glomerata* (cf. Table 1) the average frequency of trivalents was 4,6, which implies that 66 per cent of the chromosomes are in associations of three. The corresponding values for the tetraploid, *Dactylis glomerata*, was found to be 3,2 and 46 per cent. In pentaploid derivatives, obtained from the combination 3n × 4n, the same values were 2,6 and 37 per cent.

It may be open to discussion whether the meiotic behaviour in the cases cited above really should be regarded as conclusive evidence of autopolyploidy. This question may be elucidated by a comparison with the meiotic behaviour in experimental autopolyploids.

When considering experimental autopolyploids, it should be noted in the first place that the maximal chromosome association, theoretically possible, never occurs in reality. The chromosome association is almost always incomplete, and this incompleteness varies considerably in different species. This is evident e. g. from the lists given by BLEIER (1934) showing chromosome association in triploids and tetraploids. A few examples, however, may be discussed in detail.

The tetraploid *Datura* shows a very high frequency of quadrivalents, but, nevertheless, the average number is lower than the maximal number. This is evident from the statement by BELLING and BLAKESLEE (1924) that the chromosomes of tetraploid *Datura* are »as a rule» joined in quadrivalents. — In tetraploid *Primula sinensis* the frequency of quadrivalents is somewhat lower, but still rather high. DARLINGTON (1931) found that the average number in this species was 10,4, the maximal number being 12. SÖMME (1930) had previously reported a much lower number. In triploid *Primula sinensis*, DARK (1931) found that the formation of trivalents was likewise incomplete, from 2—5 univalents being present.

In *Solanum lycopersicum* different workers have obtained rather different results. JØRGENSEN (1928) observed a high frequency of trivalents in the triploid but very few, generally 1—2, quadrivalents in the tetraploid. LESLEY and LESLEY (1930), on the other hand, found a high percentage of quadrivalents in their tetraploid. LINDSTROM and KOOS (1931) got the same result, but LINDSTROM and HUMPHREY (1933) again report that at diakinesis and I—M only bivalents are present. Finally, UPCOTT (1935) has re-investigated triploid and tetraploid *Solanum lycopersicum* and finds that the average number of configurations per cell is 4,9 trivalents in the triploid and 3,8 quadrivalents in the tetraploid.

DARLINGTON (1933) has studied chiasma frequency and configura-

tions in an autotetraploid derivative from the cross *Avena strigosa* × *barbata* (cf. above p. 283) and finds that in the tetraploid about two thirds of the chromosomes form quadrivalents, the rest usually bivalents. Consequently, even in this case the formation of quadrivalents is not so high as theoretically possible, in spite of a relatively high chiasma frequency in the diploid. — In tetraploid *Narcissus pseudonarcissus*, NAGAO (1933) found that the maximum association, 7_{IV}, was only present in 8,42 per cent of the cells. According to his Table IX, p. 119 (l. c.) the average number of quadrivalents per cell was about 5,2. — Quite similar cases are represented by tetraploid *Canna aureovittata* (HONING, 1928) and tetraploid *Zea* (cf. SHARP, 1934, p. 351). — SHARP (l. c.) also cites a number of other tetraploids, which behave in the same way.

In the cases cited above the number of quadrivalents is very variable but on the average rather high, and it is only rarely that the quadrivalents are completely replaced by bivalents. In tetraploid *Solanum nigrum*, however, the situation seems to be different. According to JØRGENSEN (1928), quadrivalents are as a rule not present, the 114 chromosomes in this type usually forming 72 bivalents. However, even in this case a few quadrivalents may be present in many of the nuclei. Nevertheless we have here a striking example of an autotetraploid, in which formation of quadrivalents is almost absent and in which meiosis is strikingly regular.

Though the average frequency of trivalents in autotriploids is higher than the frequency of quadrivalents in autotetraploids, it is generally far from complete. The situation in triploid *Primula sinensis* and triploid tomato has already been mentioned. Further, in triploid *Zea*, MC CLINTOCK (1929) found that 1—4 bivalents and a corresponding number of univalents were as a rule found at I—M, though often complete formation of 10 trivalents could be observed. In triploid *Narcissus tazetta*, NAGAO (1933) reports that the number of trivalents ranged from 7 to 10, only 23 cells out of 57 showing complete formation of trivalents (10_{III}). A similar state of things was met with in triploid *Narcissus pseudonarcissus* ($n = 7$). Seven trivalents (complete association) may occur but this was observed in only 6,38 per cent of the cases. Four trivalents was the most usual number.

The meiotic conditions in experimental autopolyploids may be summarized in the following manner: The degree of association is widely different in different species, ranging from almost complete bivalency (*Solanum nigrum*) to almost complete quadrivalency (*Datura*). In some

species (*Solanum lycopersicum*, *Primula sinensis*), rather different degrees of association has been reported by different workers. This is probably due to differences in the strains used, to environmental conditions and probably also to a varying ability of detecting quadrivalents.

Returning to those chromosome races, which show multiple chromosome associations at meiosis, it is quite obvious that in this respect they are strikingly similar to the experimental autopolyploids. The data are not sufficient to allow a statistical comparison, but it should be borne in mind that in several cases reported the frequency of quadrivalents was found to be just as high as in experimental autotetraploids. Further, in spontaneous triploids (as in *Tradescantia*) or in such triploids as were produced by crossing 2n and 4n races the meiotic behaviour is of exactly the same type as in true autotriploids. Consequently, we may draw the conclusion that *in most polyploid intraspecific chromosome races chromosome association at meiosis is of the same type as in experimental autopolyploids.*

In the preceding chapters it has been demonstrated that, as regards morphology, physiology and incompatibility, there is a striking similarity between polyploid intraspecific chromosome races and experimental autopolyploids. Now this similarity has been extended to the type of chromosome association at meiosis, which may be regarded as the most important criterion of autopolyploidy. This being the case, the conclusion can now scarcely be avoided that *most polyploid intraspecific chromosome races are autopolyploid.*

As I am aware that the parallelism in chromosome behaviour may be open to some criticism, the conclusion may be supported by the following arguments.

Chromosome pairing, no doubt, in most cases indicates homology. Non-homologous pairing during prophase has been described for *Zea* by Mc CLINTOCK (1933) but is probably of minor importance, as it seldom persists to first metaphase. It is also true that many different environmental or genotypic conditions may disturb or completely prevent the pairing of homologous chromosomes (cf. FEDERLEY, 1932), but when pairing does occur, the pairing chromosomes are at least partially homologous (SAX, 1935). CLAUSEN (1931 b) holds the same opinion. Non-conjugation does not necessarily mean non-homology, but conjugation is a strong indication of homology.

Therefore, when in a tetraploid chromosome race quadrivalents are frequent, this may be deemed to prove that the race in question has four genomes, which are either identical, completely homologous or partially homologous. — Is it correct to regard such a type as being

autopolyploid? In order to answer this question we must briefly consider the difference between auto- and allopolyploidy.

These terms have been used in a somewhat different sense. Firstly, some authors evidently claim that autopolyploids should have *identical* genomes, whereas according to other authors the genomes of autopolyploids may be only *homologous*. Secondly, it may be difficult to decide what the term homologous really means.

v. WETTSTEIN (1927) includes tetraploid *AAAa* and *Aaaa* types, which are otherwise quite homologous, in the category »Polyploide Bastardrassen» in contradistinction to »Polyploide Rassen reiner Linien». These categories most probably correspond to allo- and autopolyploidy respectively. DARLINGTON (1932, p. 169) seems to be of the same opinion and says that autopolyploids have *identical* sets of chromosomes, whereas allopolyploids are the products of doubling in hybrids. SANSOME and PHILP (1932, p. 178), however, define autopolyploids as having *homologous* sets of chromosomes, allopolyploids dissimilar sets. In the chapter dealing with inheritance in autopolyploids the authors further show that they do not consider gene differences as sufficient to transfer autopolyploidy into allopolyploidy. SHARP (1934) seems to hold a similar opinion and says (l. c. p. 348) that in autoheteroploid types the chromosomes of only one kind of set are involved. »For example, a plant with three sets which are alike (within the usual specific limits) is an autotriploid.»

SIMONET (1935) has discussed the same terminology and defines autopolyploids as types »dans lesquels c'est un même groupe de chromosomes qui est répété plusieurs fois». The same author has further introduced the terms »allopolyploides isochromosomiques» and »anisochromosomiques». Allopolyploids of the first kind are those which have arisen after crosses between closely related species, which have the same chromosomal organisation but are genetically different. Allopolyploids of the second kind have arisen from species, which have structurally different chromosomes. It is not clear from these definitions whether the author considers autopolyploids to have identical or only »homologous» genomes. The latter alternative seems to be most probable, but in such a case it will be very difficult to draw a boundary-line between autopolyploids and »allopolyploides isochromosomiques».

The only distinction which is quite clear-cut is between absolute identity and dissimilarity of the genomes. This distinction, however, has a more logical than biological value, since slight gene differences in the genomes do not influence the typical morphological and physio-

logical properties of autopolyploids. In my opinion it would be better, from a biological point of view, to draw the boundary-line between auto- and allopolyploidy in such a way that it separates structural differences from mere gene differences. Consequently, we may make the following definition: *the genomes of autopolyploids are structurally identical but may be genetically different. In connection with this structural identity the corresponding (homologous) chromosomes of different genomes have an equal capacity of pairing and crossing over with each other in any combination. Allopolyploidy, on the contrary, involves structural differences between some of the genomes.*

I am aware that the two categories, gene differences and structural differences, cannot be sharply distinguished, but at any rate the definition given may have a temporary value and correspond to the opinion now generally prevailing.

It should be pointed out that the original conception of autopolyploidy, as defined by KIHARA and ONO (1927), is rather broad. It is true that the authors define autopolyploidy as »die Verdoppelung desselben Chromosomensatzes» but as examples of autopolyploidy are given not only WINKLER's gigas forms of *Solanum* but also LJUNGDAHL's *Papaver* species, which on account of their autosyndesis are regarded as autopolyploid. It is highly probable that the genomes in the latter case are not genetically identical but only homologous.

After this terminological discussion we are in a position to answer the question, raised above (p. 309), whether a frequent occurrence of quadrivalents in a tetraploid chromosome race is a reliable criterion of autopolyploidy. — According to the arguments given above, autopolyploidy means genetic homology and structural identity. Chromosome pairing is only possible between chromosomes or parts of chromosomes having the same structure. Consequently, chromosome association of the type mentioned must be taken to show that the race in question is autopolyploid or at least partially autopolyploid.

It is true that structural changes such as segmental interchange between non-homologous chromosomes may lead to associations of more than two chromosomes. It is very unlikely, however, that such changes are responsible for the multivalents observed in polyploid chromosome races. Firstly, these multivalents are always found in the polyploid, not in the diploid races, secondly, the number of chromosomes in each association generally corresponds to the degree of polyploidy present.

Before concluding this chapter, it remains to consider those poly-

ploid chromosome races which do *not* show signs of autopolyploidy at meiosis. These cases are enumerated under the headings 3) and 4) in the summary on p. 305. — Three cases mentioned under 3) are said to be probably autopolyploid though no multivalents occur. The first of these cases (No. 13) refers to the *Nasturtium* races, described by MANTON (1935). In this species the chromosomes are very small and the chiasma frequency low. Further, as the three races are morphologically very similar, and no related species are known, which might explain a possible allopolyploidy, the author concludes that, in all probability, it is a question of autopolyploidy. This seems rather likely, especially since experimental autopolyploids almost without multivalents are known (*Solanum nigrum*, cf. above). — In the next case, No. 50, which refers to *Chrysanthemum*, there is also strong evidence of autopolyploidy, though not on account of multivalents at meiosis. SHIMOTOMAI (1933) has shown that in this genus autosyndesis is very frequent in certain interspecific crosses. This will be further discussed below (p. 336). The same thing is true of the third case belonging to this category. In *Betula* (Case 56), HELMS and JØRGENSEN found autosyndesis in a hybrid between *B. verrucosa* ($n = 14$) and *B. pubescens* ($n = 28$), 21 bivalents being formed at meiosis.

In the summary, p. 305, five cases are mentioned under the heading No. 4, in which the absence of multivalents at meiosis may be taken as evidence of allopolyploidy. Of these cases, 4 and 44 refer to *Phleum alpinum* and *Phleum pratense* respectively. The cyto-genetic evidence available (GREGOR and SANSOME, 1930; MÜNTZING, 1935) really indicates that the polyploid races of these species contain different genomes. However, it has also been shown (cf. MÜNTZING, l. c. p. 133) that these genomes are not sharply differentiated but partially homologous. Multivalents have been observed in certain hybrids and hybrid derivatives.

The genomes of the polyploid chromosome races in *Viola Kitaibeliana* (Case 7) are also partly homologous. The races, which are approximately hexaploid, have the constitution *ABC*, but the race with the highest chromosome number, *nana* ($n = 24$), is supposed to have two *C* genomes and the formula *ABCC* (CLAUSEN, 1931 b). — Concerning the tetraploid *Campanula rotundifolia* (Case 42), BÖCHER reports that only bivalents are found at meiosis. As only a very limited cytological material seems to have been available in this case, the absence of quadrivalents may be registered with some hesitation.

In Case 58, finally, the hexaploid type, *Festuca arundinacea*, forms only bivalents at meiosis, but as in *Phleum pratense* there is again

evidence that the genomes are at least partly homologous. PETO (1933) reports that in the F_1 hybrid, *Lolium perenne* × *Festuca arundinacea*, a rather marked autosyndesis of the *arundinacea* chromosomes occurs. A maximum of 7_{II}, i. e. 50 per cent of the chromosomes, may be expected, but only 32,4 per cent of the chromosomes remained unpaired, the rest forming bivalents and larger associations.

Thus, though a few cases occur, in which the absence of multivalents indicates allopolyploidy, these are only exceptions and in some cases even uncertain exceptions to the rule that polyploid intraspecific chromosome races are generally autopolyploid.

In quite a large number of cases meiosis has not yet been studied (cf. summary, p. 305), but even in some of them evidence of autopolyploidy is available. For instance, in *Iris* and *Vallisneria* (Cases 39 and 54), the morphology of the chromosomes strongly indicates that the tetraploid races are autotetraploid. In both cases several different chromosome types may be distinguished, and these are represented twice in the diploid, four times in the tetraploid. For details I must refer the reader to the papers cited in Table 1.

Similar chromosome morphological observations in *Silene ciliata* (Case 10) support the evidence of autopolyploidy, obtained from the study of meiosis. BLACKBURN (1933) observed that the diploid race had satellites on two chromosomes, whereas the number of satellites was four in the tetraploid. — Finally, it should be mentioned that in most cases, in which no other evidence is available, the striking morphological similarity between the different races has convinced the respective authors that they had to deal with auto- and not with allopolyploidy (e. g. Cases 9, 17, 18, 21, 24, 41, 53). It is to be expected that upon closer examination most of these cases will be found to be just as typical examples of autopolyploidy within the species as the other cases discussed in this chapter.

8. FERTILITY AND CONSTANCY IN INTRASPECIFIC CHROMOSOME RACES AND EXPERIMENTAL AUTOPOLYPLOIDS.

It is generally assumed that the presence of multivalents at meiosis must lead to meiotic irregularities and hence to reduced fertility and inconstancy. Multivalents were found to be frequent in polyploid chromosome races, but in spite of that, fertility in such races does not seem to be impaired. Unfortunately very little is known about fertility in intraspecific chromosome races, but the evidence available strongly in-

dicates that *fertility is generally quite good in polyploid as well as in diploid races.*

Of the 58 cases cited in Table 1 only 13 have been studied as to fertility. These cases may be grouped under the following headings:

1) *The polyploid races are quite fertile in spite of multivalents at meiosis.*
   Cases: 1, 10, 15, 17, 27, 47, 57.
2) *The polyploid races are quite fertile and have no multivalents at meiosis.*
   Cases: 4, 13, 44.
3) *The polyploid races are quite fertile, meiosis not studied.*
   Cases: *16*, *21*.
4) *The polyploid race is possibly partially sterile.*
   Case: 19.

As to the first category the autotetraploid gigas race in *Allium* (Case 1) has very good fertility (more than 90 per cent good pollen) and is exceedingly fruitful. It produces a larger number of seeds per inflorescence than diploid races (l. c. p. 91). This good fertility coincides with the fact that meiosis in the tetraploid is very regular, in spite of the quadrivalents present. The pollen grains were always found to have 16 chromosomes, and thus this race will also be constant. It may be remembered that this type, detected by TURESSON (1931 a), grows abundantly along the shores of Lake Teletskoje in East-Altai. No doubt it is capable of constant reproduction by seed.

In *Silene ciliata* (Case 10), both the tetraploid and the 16-ploid races have high fertility. Italian tetraploids were found to be somewhat unstable, plants with 49 and 50 chromosomes instead of 48 being observed. This cytological instability is probably due to the presence of quadrivalents, which occasionally cause an irregular disjunction of the chromosomes. Nevertheless, the tetraploid types, according to BLACKBURN (l. c.), seem to be the successful forms in Italy today. — In spite of the high chromosome number in the 16-ploid type chromosome disjunction, as a rule, was found to be regular.

The tetraploid race of *Biscutella laevigata* (Case 15) is evidently also somewhat unstable. As in *Silene ciliata* the presence of quadrivalents may cause slight meiotic irregularities. These are probably responsible for the occurrence of aberrant tetraploids with 37, 35 and 34 chromosomes instead of the typical number 36. According to

MANTON (1934, Tables 2 and 4), the percentage of such aberrants is about twenty. One progeny studied was obtained from a plant, which was itself aberrant. This indicates that some aberrant plants are viable and set seed in the wild state. Nevertheless, in spite of the relatively high frequency of aberrants, the typical number of the tetraploid variety is no doubt 36 (l. c., Table 4). The diploid race uniformly showed the number 18 (l. c., Table 3).

Meiotic irregularities in combination with the production of aberrants also characterize different *Pentstemon* types studied by CLAUSEN (1933). In *Pentstemon azureus* the hexaploid subspecies *typicus* was found to be characterized by multivalents, irregular meiosis and the occurrence of aberrants with somewhat deviating chromosome numbers. The related amphidiploid, *P. neotericus*, behaves in the same way. — In tetraploid *Pimpinella saxifraga* (Case 30), HÅKANSSON (1933) noticed a strong morphological variation in the small area in which the tetraploids were growing. This variation may be connected with the observed presence of multivalents at meiosis and the production of aberrants as a consequence of irregular meiosis.

Case 17, the *Galium* species, is not so well known as most of the preceding cases, but in his preliminary report FAGERLIND (1934) remarks that the polyploid *Galium* races have normal fertility. This is supposed to be due to the relatively low frequency of multivalents in *Galium*. — With regard to *Tradescantia* (Case 27) it is emphasized by ANDERSON and DIEHL (1932) that in this genus propagation by seed is much more important than vegetative reproduction. This is true also of the tetraploid types, which consequently, in spite of a high frequency of multivalents, must have quite good fertility. — In the tetraploid *Empetrum hermaphroditum* (Case 57) fertility is also excellent and propagation is chiefly by seed. The diploid *Empetrum nigrum*, on the other hand, has a more pronounced tendency to vegetative propagation.

In *Dactylis* (Case 47) reproduction is exclusively by seed, and both diploids and tetraploids are perfectly fertile. The tetraploid *glomerata*, however, is not cytologically stable. Quadrivalents are frequent in commercial varieties as well as in an absolutely wild biotype from Siberia (MÜNTZING, unpublished results). Owing to complete terminalisation and, as a rule, zig-zag arrangement at first metaphase, disjunction is usually quite regular. Gametes with deviating chromosome numbers are formed, however, in a low frequency, and in the progeny a somewhat varying percentage of aberrants may be observed. Com-

pared to the normal plants with exactly 28 chromosomes these aberrants are on an average inferior in vigour and fertility.

From the cases cited above it is obvious that the presence of multivalents at meiosis does not necessarily involve a decrease in fertility. On the other hand it is comprehensible that those polyploid races, which have no multivalents at meiosis, should be fertile, thanks to the regularity guaranteed by the exclusive presence of bivalents. In the tetraploid races of *Phleum alpinum* and *Nasturtium officinale* (Cases 4 and 13) this has indeed been found to be true. The same situation is met with in the hexaploid *Phleum pratense* (Case 44). — Only in one single case (No. 19) does the tetraploid race seem to have a lower fertility than the diploid. HAGERUP (1933) reports that in *Vaccinium uliginosum* seed setting is better in the diploid arctic type than in the tetraploid race. It remains to be studied, however, whether this decrease in fertility is really caused by quadrivalents and meiotic irregularities.

In the other cases of intraspecific chromosome races (with the exception of Cases 16 and 21, in which fertility is reported to be good) nothing is definitely known concerning fertility and its relations to the mode of meiosis. It is highly probably, however, that fertility in practically all these cases is good, since, with few exceptions, they are known to be propagated by seed and not vegetatively. This is evident in particular with regard to those species which are annual (Cases 2 and 7, partly also Case 17).

Of the 58 cases cited in Table 1 only the following are known to have a more or less complete vegetative propagation: Nos. 13 (*Nasturtium*), 16 (*Narcissus bulbocodium*) and 54 (*Vallisneria*). In the first two of these cases, however, propagation by seed is also important. Only the triploid *Nasturtium* race is forced to exclusive vegetative propagation, the diploid and tetraploid races having normal seed production. Further, multivalents do not occur in the polyploid races of this species. Hence this case cannot be taken as evidence that vegetative propagation is necessary in order to preserve the occurrence of multivalents at meiosis. In the other case, *Narcissus bulbocodium*, FERNANDES (1934) stresses the good fructification of several races belonging to this species.

The good fertility in polyploid chromosome races is in contrast with the conditions in experimental autopolyploids, in which fertility is on an average rather poor. SANSOME and PHILP (1932, p. 181) have

tabulated the degree of fertility in a number of diploid forms and their autotetraploid derivatives. The following autotetraploids were found to have considerably lower seed production than the corresponding diploids: *Solanum lycopersicum*, *Datura stramonium*, *Primula sinensis* and *Campanula persicifolia*. Judging from the figures given, the degree of reduction, however, is rather different in the four species. In *Datura* and *Solanum* the seed set in the tetraploid is only about 20 per cent of that in the diploid. In *Campanula* the corresponding figure is 46 per cent and in *Primula sinensis* about 70 per cent. Reduced fertility in autotetraploids is further reported for *Solanum nigrum* (JØRGENSEN, 1928, p. 162), *Solanum pimpinellifolium* (LINDSTROM and HUMPHREY, 1933), *Canna aureo-vittata* (HONING, 1928), *Oenothera Lamarckiana* (cf. WINKLER, 1916, p. 509) and *Oenothera franciscana* (DAVIS, 1933).

The gigas type of *Cleome spinosa*, studied by UFER (1927), had on an average less good pollen than the diploid. Single gigas plants, however, had even better pollen fertility than the diploids. Seed production, too, was found to be very variable. Some gigas plants produced a relatively large number of seeds, other individuals had quite poor seed setting.

Reduced fertility in autotetraploids has generally been assumed to be due to meiotic irregularities, caused by the occurrence of quadrivalents (cf. DARLINGTON, 1932, p. 179; SANSOME and PHILP, 1932, p. 182; SHARP, 1934, p. 352). This is certainly true in part, but we have reason to believe that the reduced fertility in experimental autotetraploids is chiefly caused by other conditions.

As discussed and exemplified by the present writer (MÜNTZING, 1930 a), sterility is of two main kinds, diplontic and haplontic sterility. Diplontic sterility means that the reproductive organs, the gones or the gametes, are defective owing to physiological disturbances in the mother individual. The gametes or microspores are killed by the mother individual, irrespective of their own constitution. In cases of haplontic sterility, on the other hand, certain classes of gametes are killed by their own lethal constitution. In autotetraploids sterility has been assumed to be of the latter kind. Evidence is now available, however, indicating that diplontic sterility in these cases must be equally or even more important.

LINDSTROM and KOOS (1931) report that in tetraploid tomato pollen fertility is good but seed setting poor, the fruits containing a high proportion of abortive seeds. The authors find that meiosis on the male side is rather regular, second metaphases with deviating chromosome

numbers being rare. This is inconsistent with the high sterility on the female side. — LINDSTROM and HUMPHREY (1933) have made similar observations with regard to *Solanum lycopersicum, pimpinellifolium* and F_1-hybrids between these species. These results strongly indicate that the low seed production in these cases is due to physiological disturbances and not to haplontic sterility. — This is especially evident when compared with the conditions in *Solanum nigrum*. As already mentioned the tetraploid form of this type is characterized by a strikingly regular meiosis (JØRGENSEN, 1928) in the pollen and almost complete absence of multivalents. Nevertheless the fruits of the tetraploid were found to contain only 10—15 seeds, the corresponding number in the diploid often being as high as 40—50. — It should also be mentioned that just the same conditions are characteristic of the amphidiploid hybrid *S. nigrum* × *luteum*. In this type meiosis is quite regular and only bivalents were observed at I—M (JØRGENSEN, l. c. p. 189). Nevertheless, fertility is rather poor, only 35 per cent of the pollen being good as compared with 90 per cent in the *nigrum* parent and 75—80 per cent in *S. luteum*. The number of seeds in the fruits of *nigrum* was 40—50. The amphidiploid had only 8—11 seeds per fruit. — It is possible, though very improbable, that meiosis on the female side of autotetraploid *nigrum* is irregular to such an extent that only a low proportion of the ovules will be functional. In other cases, however, there is direct evidence that the poor seed production is due to physiological disturbances and consequently to diplontic sterility.

In the tetraploid *Canna aureo-vittata*, HONING (1928, p. 9) has observed typical degeneration phenomena at meiosis which evidently have nothing to do with the occurrence and disjunction of the quadrivalents. This autotetraploid is also highly sterile. — It has been mentioned that in the gigas type of *Cleome spinosa* different individuals had quite different fertility (UFER, 1927). Now, in tetraploids with poor pollen fertility the pollen was visibly defective to the naked eye, being pale yellow instead of bright yellow as the good pollen. In all probability this difference is chiefly due to physiological disturbances in the mother plant and not to meiotic irregularities followed by haplontic sterility. The same probably holds true with regard to sterility in tetraploid *Oenothera fransiscana*. According to DAVIS (1933), this type has only 20 per cent good pollen, which is supposed to be due to various meiotic irregularities. However, triploid individuals of the same species were found to have *better* pollen fertility than the tetraploid. This is a strong indication that sterility in these types is not

primarily caused by the presence and irregular disjunction of multivalents but by physiological disturbances which are more pronounced in the tetraploid than in the triploid.

In conclusion, the paper by UPCOTT (1935) should be considered. This author has re-investigated the cytology of triploid and tetraploid *Solanum lycopersicum* and finds that the low seed production in the tetraploid may be explained by the observed frequency of non-disjunction from quadrivalents. Sixty-three per cent of the II—M plates were found to have the normal chromosome number 24 and thus about 37 per cent of the gametes would be numerically unbalanced (according to Table VII, p. 13, in the paper cited; other workers have found a higher proportion of balanced gametes). Since part of the gametes that are numerically balanced may be genetically unbalanced, the author estimates the proportion of functional gametes at about 40 per cent or somewhat more, only 25 per cent of the pollen being visibly bad. Combination of these gametes with each other would give the observed proportion of seed setting, i. e. 20 per cent of the seed production found in the diploids. — This conclusion, however, can scarcely be accepted, firstly because the proportion of functional pollen grains would suffice to fertilize all functional ovules, secondly because haplontic sterility is generally less pronounced in the ovules than in the pollen. — Consequently, the only possible explanation seems to be that physiological disturbances and diplontic sterility are also, and perhaps chiefly, responsible for the low fertility in this case, just as in the other cases mentioned above.

From the previous examples it is evident, that with respect to the average degree of fertility, experimental autotetraploids and polyploid chromosome races are rather different. What is the cause of this difference, and why are polyploid chromosome races more fertile than experimental autopolyploids? To answer this question we must resort to a hypothesis, which, however, seems rather plausible. The wild chromosome races have been subjected to natural selection, or more correctly, are the successful survivors from a much larger material. Only part of this species material has been able to produce polyploid races with a certain minimum degree of fertility. — The experimental material, on the other hand, is extremely limited and has not been subject to selection. It is striking, however, that the few experimental autotetraploids known show a considerable variation in fertility, which would be important if these types were tried by natural selection. It is uncertain whether any of those types known at present would be

able to survive under natural conditions, but the fact that some of them have much better fertility than others strongly indicates that in a larger material successful tetraploids with good fertility would appear.

As emphasized above the degree of fertility in experimental autotetraploids is not necessarily correlated with the frequency and behaviour of the quadrivalents. The physiological condition of the mother plant seems to be more important than the constitution of the spores, and this physiological condition seems to vary from species to species. This variation is more comprehensible when compared with the morphological results of chromosome doubling. As already discussed in a previous chapter, autotetraploids are generally rather vigorous, but in some cases (p. 286) the tetraploid is not superior or even inferior in vigour compared to the diploid. — Unknown factors in the constitution of different species evidently control both vigour and fertility of the autotetraploid products in a way that cannot be predicted.

In the moss species, v. WETTSTEIN (1927, 1928) has observed that autopolyploid races are more or less unstable and tend to revert to the normal chromosome number both somatically and generatively. The tendency to back-regulation increases with the valency and is rather different in different species. Probably it is this unstableness which makes v. WETTSTEIN inclined to regard autopolyploidy as of little or no evolutionary significance (cf. the introduction to this paper, p. 264).

In the higher plants the situation is different and the autotetraploid types are generally rather stable. It is true that WINKLER (1922) observed some somatic aberrations in his tetraploid *Solanum lycopersicum*, but the chromosome number was found to be constant after propagation by seed. JØRGENSEN (1928) has confirmed this constancy and reports that all the tetraploids studied by him, including tetraploid *Solanum lycopersicum* and *nigrum*, gave constant offspring with the tetraploid chromosome number. — The tetraploid form of *Oenothera biennis* is described by STOMPS (1925) to be »tout à fait constante» and the same is true of the tetraploid race of *Oenothera fransiscana*, which was found to be essentially constant in four generations (DAVIS, 1933).

The constancy of tetraploid *Datura stramonium* has been carefully studied by BELLING and BLAKESLEE (1924). A tetraploid plant with 48 chromosomes was self-fertilized and gave 62 daughter plants, 55 of which, i. e. 89 per cent, had the same chromosome number and constitution as the mother plant, whereas 7 plants were aberrants. Five of

these seven plants had 2n = 49, one 2n = 47 and one was found to be a 4n + 1 — 1 individual. The high degree of constancy in this case is remarkable, as the frequency of quadrivalents in tetraploid *Datura* is very high (cf. p. 307). It was also observed that only in 73,2 per cent of the p.m.c. the chromosome distribution was 24—24. About 25 per cent of the pollen grains obtain 23 or 25 chromosomes. As the percentage of plants with the normal chromosome number and constitution was found to be higher than the percentage of normal (male) gametes, selection of gametes or zygotes may be responsible for the fact that morphological and cytological constancy is in the main upheld. This is also indicated by the fact that, in spite of chromosome elimination at meiosis, most of the aberrant plants had a higher number of chromosomes than 48.

It is well-known that such aberrants in *Datura* and in other genera are inferior in viability and fertility. From my own experience I may mention that the aberrants in *Dactylis glomerata*, with the chromosome number ranging from 27 to 31, are progressively inferior in vigour and fertility the more the chromosome number departs from the normal number 28. Consequently, even if such aberrants are formed, due to incomplete gametic and zygotic selection, they cannot compete with the normal individuals. The typical chromosome number will in this way be upheld in spite of the formation of a certain percentage of aberrants in each generation. — *Dactylis glomerata*, which together with *D. Aschersoniana* represents one of the cases in Table 1, thus behaves in just the same way as the autotetraploid *Datura*. The same is true of some other polyploid chromosome races already mentioned (*Silene ciliata*, *Biscutella laevigata* and *Pentstemon azureus*). Other polyploid chromosome races also seem to be quite constant, like several experimental autotetraploids. This constancy may, for instance, be due to the following different conditions: a) only bivalents occur at meiosis, which is consequently quite regular, b) quadrivalents occur, but chromosome distribution is quite regular thanks to complete terminalisation and regular zig-zag arrangement, c) gametes with deviating chromosome numbers are formed but do not give rise to aberrants on account of elimination of aberrant gametes and zygotes. In the last-mentioned case fertility will be somewhat reduced, but this may be counterbalanced by increased vigour, new physiological properties or other advantages of the polyploid condition.

This chapter may be concluded by the statement that *as regards constancy polyploid chromosome races and experimental autopoly-*

ploids behave in the same way. As far as fertility is concerned, however, they are different, but this difference seems explicable by the fact that the chromosome races in contradistinction to the experimental autopolyploids have been subject to natural selection. They represent the successful survivors from a larger material. It is also possible that secondary processes of various kinds have caused an increase in fertility.

9. INTRASPECIFIC CHROMOSOME RACES IN APOMICTIC SPECIES.

The discussion of intraspecific chromosome races has hitherto been based on evidence obtained from amphimictic species, capable of sexual reproduction. As a supplement to the conclusions reached by means of this material a number of apomictic species will be briefly considered. As regards morphology, ecology and meiotic behaviour these are evidently very similar to the amphimictic species.

The parthenogenetic animals *Artemia salina* and *Solenobia triquetrella* have already been mentioned above in the chapter on the physiological consequences of chromosome doubling. Besides the striking physiological differences there also occur morphological differences, the polyploid races being gigas types. — Concerning *Artemia*, ARTOM (1928) states that the gigantism of the tetraploid *Artemia* race is obvious, especially as regards such organs as are composed of a fixed number of cells. Cell size is here, as always, positively correlated with chromosome number. GROSS (1932) has also noticed that octoploid individuals of *Artemia salina* finally reach a greater size than diploids.

In *Solenobia*, SEILER (1927) has observed that the tetraploid parthenogenetic females are much bigger than the diploid sexual ones and the pupae of the tetraploids were found to have twice the volume of the pupae of the diploids. — The tetraploid, parthenogenetic type seems to be more successful in the struggle for life than the diploid type. SEILER reports (l. c. p. 427) that the parthenogenetic race has a wide distribution and is easy to find almost everywhere, in contradistinction to the sexual diploid, which could only be obtained from one special locality.

These conditions are very similar to the situation met with in *Chara crinita* (ERNST, 1918). This species comprises both sexual and parthenogenetic biotypes, the former having 12 chromosomes, the latter 24. The sexual form evidently cannot successfully compete with the parthenogenetic race, which has a much larger distribution and seems

to invade localities in which the sexual race grows. The parthenogenetic race has also been able to penetrate into areas, especially in northern Europe, in which the sexual race cannot exist. In correspondence with the higher chromosome number the parthenogenetic race is morphologically a gigas type in comparison with the haploid sexual type (l. c. pp. 72—73). As is well-known, ERNST (l. c.) considers the parthenogenetic *Chara crinita*, as well as most other apomictic species and biotypes, to be of hybrid origin. HOLMGREN (1919, p. 111) has critizised this theory as regards *Chara crinita*, and, indeed, in the light of recent results with other species it seems highly probable that the parthenogenetic race is auto- and not allopolyploid, in the same manner as the parthenogenetic races of *Artemia* and *Solenobia*.

The majority of the apomictic plants may be of hybrid origin, but a few cases are known, however, which are probably autopolyploid. From my own experience I may mention the pseudogamous *Potentilla* species (MÜNTZING, 1928, 1931 a), in which the presence of multivalents at meiosis in the polyploid types indicates autopolyploidy. In these species, at least *P. argentea* and *Tabernaemontani*, the hypothesis of autopolyploidy is further supported by the occurrence of a marked positive correlation between chromosome number and vigour. This holds good with regard to diploid, hexaploid and octoploid *argentea* as well as hexaploid and duodecaploid *Tabernaemontani* ($2n = 42$ and 84 respectively). The last mentioned biotype is in all respects a very marked gigas type as compared with the hexaploid biotype.

According to BERGMAN (1934), triploid apomictic biotypes of *Hieracium umbellatum* are also probably autopolyploid and have presumably arisen from the union of one reduced and one unreduced gamete. The autopolyploid nature of these biotypes is probable from chromosome morphological evidence and from the occurrence of trivalents at meiosis in the pollen mother cells.

TURESSON (1930, 1931 b) has studied the distribution, morphology and chromosome number in viviparous biotypes of *Festuca ovina* and finds that the different chromosomal types ($2n = 21, 28, 42$) have different distribution and present quantitative morphological differences. The type with the highest chromosome number is most vigorous, the tetraploid is intermediate. This positive correlation between chromosome number and vigour strongly indicates autopolyploidy and this possibility is further supported by the fact that the degree of vivipary is proportional to the chromosome number. — The different distribution

of the chromosomal types also accords very closely with the general behaviour of polyploid chromosome races.

Examples of different ecology and slight, quantitative morphological differences in combination with different chromosome numbers may also be taken from the genera *Taraxacum* and *Rubus*. According to GUSTAFSSON (1935, and verbal information), there are in *Taraxacum* pairs of apomictic species, which are morphologically very similar, but which have different chromosome numbers, *e. g. T. obliquum* (triploid) and *platyglossum* (tetraploid), *T. laetum* and *obscurans* ($2n = 24$ and 32 respectively). The differences in chromosome number are in these cases correlated with slight, mainly quantitative differences and with a change in ecology and distribution. Similar conditions are also met with in the genus *Rubus* (l. c. p. 329). Some apomicts occurring in the east of Sweden appear in the west in a phenotypically identical (?) form but with a higher chromosome number.

In the genus *Sorbus*, LILJEFORS (1934) found that the polyploid species and varieties are probably apomictic. *Sorbus aria* has $n = 17$ but *S. aria* subsp. *norvegica* is a tetraploid with $n = 34$. According to LILJEFORS, this subspecies is most probably an autotetraploid derivative of diploid *aria*. It has a high frequency of quadrivalents at diakineses. Judging from the name it may also have a different geographical distribution.

Though rather few and incomplete, the data presented above indicate that as regards morphology, ecology and chromosome association (in the p.m.c.) chromosome races in apomictic species have the same essential properties as those found in chromosome races of sexual species. We meet again quantitative morphological differences, positive correlation between chromosome number and vigour, changed ecological properties and finally cytological evidence of autopolyploidy. It is only with respect to the result of crosses between the races that no data are available, owing to the mode of propagation.

III. THE RELATION BETWEEN INTRA- AND INTERSPECIFIC POLYPLOIDY.

From the report given above, concerning intraspecific chromosome races, it is evident that the occurrence of such races both in amphimictic and apomictic species is an important phenomenon, which merits careful attention. Especially interesting is the fact that the ecological range of the species will generally become much greater when poly-

ploid intraspecific races arise. Thanks to more thorough studies of the chromosomal constitution of the species, the number of such cases seems to be rapidly increasing. Under such circumstances this phenomenon must be considered to be a most important factor in the evolution *within* the species. The question must then naturally be raised, whether the formation of polyploid chromosome races has anything to do with the formation of new species. In other words, *what are the relations between intra- and interspecific polyploidy*?

1. MORPHOLOGY AND ECOLOGY.

Considering morphology first, it has been mentioned above (p. 267) that there is no clear-cut boundary between intraspecific chromosome races and distinctly separated species. On the contrary, the transitions are evidently quite continuous. Of the cases cited in Table 1 (p. 270) those given in the latter part of the table (Nos. 43—58) represented a number of »dubious» cases. These consist of collective species, or types now considered as distinct though closely related species, which, however, were formerly included in the same species unit. Details concerning these cases have been given above on pp. 267—268 and 279. It should be emphasized that the boundary-line between the two categories in Table 1 is rather arbitrary. Several of the cases 1—42 are represented by races, already now recognized by taxonomists as distinct varieties or subspecies. It is highly probable that some of them, after closer taxonomical examination, may be raised to the rank of independent species (*e. g.* in Cases 3, 7, 16, 18, 35). In other cases, on the contrary, the chromosome races seem to be so alike morphologically that probably they will not be recognized as taxonomical units at all, at any rate not as separate species. Such races are, *e. g.* represented by Cases 17 (partly) and 27.

Hence we have reason to believe that the degree of morphological difference between the chromosome races is decisive for their taxonomical treatment. If a new polyploid chromosome race is formed and observed by taxonomists it will get a taxonomical value, which is proportional to the degree of morphological difference and to the sharpsightedness of the observer. If also the new ecological properties and the new distribution are observed, the race will probably get a fairly high taxonomical value and even be considered as a new species, unless the morphological differences are not too slight. Under such circumstances it is evident that some of the plant species now described must be regarded as nothing but autopolyploid chromosome races.

Concerning the conceptions »race» and »species» in this connection, it should be mentioned that »race» is used as a quite neutral term, the meaning of which is clear from the previous discussion, and by »species» I mean the taxonomical species. In the present paper I will refrain from a discussion of the proper taxonomical treatment of the chromosome races and from terminological problems connected therewith. At present I only wish to emphasize the continuous transitions between such chromosome races, which have escaped the attention of taxonomists, to species which are distinctly separated and which are members of a polyploid series within the genus. *This continuity strongly indicates that the formation of autopolyploid chromosome races is an important factor in the evolution of species.*

This theory is strongly supported by other evidence. The ecological properties have already been called attention to. It has been demonstrated (cf. above p. 288) that chromosome races are generally ecologically different and very often have different geographical distribution. As is well-known, these properties are also quite characteristic with respect to different species in a genus. As regards ecology chromosome races and distinct species consequently behave in exactly the same way.

In this connection it should be remembered that polyploidy seems to be an advantageous property, which may cause an increased adaptibility and greater resistance to unfavourable environmental conditions. This has been exemplified above (pp. 292 and 299—300) both in the case of chromosome races (*e. g. Nasturtium, Biscutella, Opuntia, Viola crassa, Eragrostis*) and in the case of the different species of a genus (*Dianthus*). As to *Dianthus*, this genus is also represented in Table 1, partly by typical intraspecific races (Case 14), partly by closely related species (Cases 48—49). — It is highly probable that the positive correlation in *Dianthus* between polyploidy and superior ecological properties is to be understood in such a way that autopolyploidy is largely responsible both for the production of races and species and for the new ecological properties of the polyploid types in this genus.

2. INCOMPATIBILITY.

Still more important than the ecological similarity between chromosome races and distinct species is their identical behaviour as regards incompatibility and sterility.

In previous papers (MÜNTZING, 1930 b, 1933 b) I have discussed the causes of complete or partial incompatibility in crosses between types

with different chromosome numbers. Such crosses generally give less good results than crosses between types with the same chromosome number. *This is true of experimental auto- and allopolyploids as well as of natural species or races, representing different multiples in a polyploid series.* In a preceding chapter (p. 300) the striking similarity in this respect between experimental autopolyploids and intraspecific chromosome races was demonstrated. The identical behaviour of allopolyploids and polyploid species has been exemplified in a previous paper (MÜNTZING, 1933 b).

It is especially interesting that this incompatibility is quite typical also in the case of autopolyploids, in which only the quantitative relations are altered. Therefore, *it is quite probable that also in the other categories mentioned it is mainly rather simple quantitative conditions, which are responsible for the barriers of incompatibility, separating the representatives of different chromosome multiples.*

Incompatibility is mainly caused by checked pollen tube growth or by zygotic lethality. As regards the latter, which seems to be the most important type of incompatibility, the present writer has attempted to supply an explanation. This theory, which is chiefly based on WATKINS' results in wheat (WATKINS, 1927) and my own observations in *Galeopsis*, was advanced in 1930 and discussed in detail in 1933. It may be summarized as follows:

The cause of the disturbed seed development is of a quantitative nature. During seed development three different tissues are in intimate contact: embryo, endosperm and the surrounding somatic tissues of the mother plant. In normal cases, i. e. in non-hybrid plants, in which all gametes have half the somatic chromosome number, the relation between the chromosome numbers of these tissues is 2 : 3 : 2. If the gametes which unite have different chromosome numbers (or more correctly: chromatin masses) these relations will be altered. This will cause alterations of the morphological and no doubt also of the physiological properties of the tissues concerned (changed cell size and rate of division) and hereby disturbances of their interrelations. The result is poor development or complete abortion of the seeds. Not only the relation between embryo and endosperm but also the chromosome number of the mother plant is significant. Further, if viable gametes with different chromosome numbers are formed by the same plant and if these gametes form zygotes and seeds, the best seed comes from the union of gametes with the same or approximately the same chromosome number. — This theory has been exemplified in detail in the

paper in 1933 b. Since then it has been further supported by the experimental results of SKALINSKA (1934) and GRAZE (1935).

It is a very striking fact that intraspecific chromosome races with different chromosome numbers were found to be separated by barriers of incompatibility and sterility, which are just as strong and pronounced as the barriers between different polyploid species. *This may be taken as indirect evidence that these species have arisen in the same way and have essentially the same constitution as the polyploid chromosome races.* Further, as the chromosome races are mainly autopolyploid this strongly indicates that the barriers between polyploid species are also caused by simple quantitative relations.

These conclusions may be supported by the results of species crosses in certain genera. In the genus *Chrysanthemum*, SHIMOTOMAI (1933) has performed numerous crosses between species which either have the same chromosome number or which differ in varying degrees in the number of chromosomes. In Table II of the paper mentioned, SHIMOTOMAI has summarized the results of his crosses without drawing any particular conclusions. An analysis of these data, however, is given in Table 3 of the present paper. The number of hybrid seedlings obtained, divided by the number of pollinated flower-heads may be taken as a measure of the result of the cross. The gametic chromosome numbers of the parents, forming a typical polyploid series, range from 9 to 45. The differences in chromosome number may thus have the values 0, 9, 18, 27 and 36.

According to Table 3, the result of the cross is on an average inversely proportional to the difference in chromosome number between the species crossed. The best result was obtained when the species had the same chromosome number (difference = 0), the average value (number of hybrid seedlings : number of pollinated flower-heads) being 16,7. This value represents the average result of 15 combinations (including reciprocal crosses). The corresponding value for 28 combinations, involving a difference of 9, was found to be 12,5. When the difference is as great as 18 the result is still poorer, the average value in this case being 2,8 (18 combinations). Extremely bad results, however, were obtained when the parents differed as much as 27 and 36 in chromosome number. Only 4 such combinations were tried and gave an average value of 1,5 (cf. Table 3).

These results may be summarized by the following statement: As the differences increase according to the series 0, 9, 18, 27, 36 the success of the cross decreases according to the series 16,7; 12,5; 2,8;

1,5; 1,5. *This result very strongly indicates that the barriers of incompatibility between these species are mainly due to purely quantitative conditions.* In the opposite case it would be impossible to understand the continuous decrease in the crossing results, which was found to be correlated with the increase of the chromosomal difference. According to our theory, the increase of this difference will cause a more and more severe deviation from the normal 2 : 3 : 2 ratio (chromosome numbers of embryo, endosperm and somatic tissues), and this will be increasingly injurious to the young hybrid zygotes.

TABLE 3. *Correlation between chromosomal difference and result of crosses in Chrysanthemum.* (*Data from* SHIMOTOMAI *1933, Tabelle II.*)

Difference in chromosome number between the species crossed	Number of hybrid plants obtained: number of pollinated flower-heads																				n	M
	0	3	6	9	12	15	18	21	24	27	30	33	36	39	42	45	48	51	54	57	60	
0	1	3	1	2	1	1	1	2	1	—	1	—	—	—	—	—	—	—	—	1		15	16,7
9	7	6	3	2	2	2	—	1	2	—	—	—	1	1	—	—	—	—	—	—	1	28	12,5
18	16	—	—	1	—	1																18	2,8
27	2																					2	1,5
36	2																					2	1,5

The correctness of this interpretation is further supported by the results of crosses with one particular *Chrysanthemum* species, *C. Makinoi.* This species, which is diploid (n = 9), was crossed as female parent to *Chrysanthemum japonense* (n = 27), *C. Decaisneanum* (n = 36) and *C. pacificum* (n = 45). The crosses gave poor results, but a few F_1-hybrids were obtained in each case. The reciprocal crosses failed altogether. The F_1-plants obtained, however, had not the expected chromosome number but a much higher one, the somatic chromosome numbers in the three types of F_1-hybrids being 63, 72 and 81 respectively. This can only be explained by the assumption that the functional ovules in the diploid parent species had the number 36 instead of 9. Now, according to our theory, the wide chromosomal differences between the species crossed (18, 27 and 36 respectively) would result in very poor hybrid zygotes. If, however, the functional ovules are tetraploid, the chromosomal differences between the uniting gametes will be much smaller (in the three crosses 9, 0 and 9 respectively) and this will completely or almost completely restore the normal 2 : 3 ratio bet-

ween the chromosome numbers of embryo and endosperm. Under such circumstances it is possible to understand that a low frequency of tetraploid ovules may be fertilized by male gametes and give rise to zygotes which are alone viable in contrast to the normal hybrid zygotes which die on account of too serious embryological disturbances. The death of these hybrid embryos has in fact been observed by SHIMOTOMAI (1933, p. 54). Hybrid embryos obtained from the cross *Makinoi* × *pacificum* (9 × 45) were observed to have 54 chromosomes in the second division, but these embryos die and only those which result from the union of gametes with approximately the same chromosome number are able to survive and give F_1-plants with an increased chromosome number. That functional reduced ovules with 9 chromosomes are really formed in *C. Makinoi* is also evident from the fact that the cross *Makinoi* (n = 9) × *indicum* (n = 18) gave a hybrid with the expected chromosome number 27. In this combination the normal ovules may function, as the difference in chromosome number between the parents is only nine.

Exactly comparable results have been obtained in several other genera. Without going into details I will only refer the reader to the cross *Fragaria nipponica* × *elatior* studied by LILIENFELD (1933), crosses between diploid and tetraploid *Zauschneria* species (CLAUSEN, KECK and HEUSI, 1934) and between diploid and hexaploid *Phleum* species (H. NORDENSKIÖLD, unpublished results, cf. above p. 302).

Before leaving *Chrysanthemum*, it should be mentioned that about the same results of the crosses were obtained, whether the species with the higher chromosome number acted as female or male parent. The average value in the first case was found to be 7,62, in the second case 8,70. These values are in both cases based on 25 cross combinations. The difference is probably not significant (the standard error could not be calculated owing to a marked skewness in both series). — Finally, an attempt was made to distinguish between those cases in which a certain difference is found between parents with low chromosome numbers or between those with rather high numbers. A difference of 9 between 9 and 18 would have a much greater effect than the same numerical difference between, *e. g.* 36 and 45. Of these 28 combinations, in which the difference is 9 (cf. Table 3), 6 combinations represent differences 18—9 and 27—18, whereas the remaining 22 combinations correspond to differences 36—27 and 45—36. The average result of the crosses was found to be 5,0 in the first case, 14,6 in the second. This indicates that it is not the numerical difference but rather the *relation*

between the chromosome numbers of the parents which is responsible for the result of the cross. The data now available, however, are insufficient to prove that definitely.

An analysis, similar to that made in *Chrysanthemum*, of the results of species crosses in a genus has also been undertaken in the case of *Dianthus*. In this genus, ANDERSSON-KOTTÖ and GAIRDNER (1931) have made extensive crossing experiments between different species and varieties having the same or different chromosome numbers. The results of these crosses are summarized in Table 1 given in the paper cited. In this table the following symbols are used: a — indicates that the cross failed altogether, a ± means that the F_1 obtained was completely sterile, a □ means that the F_1 obtained was partly sterile and a ○, finally, that it was fertile.

TABLE 4. *Correlation between chromosomal difference and result of crosses in Dianthus.* (*Data from* ANDERSSON-KOTTÖ *and* GAIRDNER *1931, Table I.*)

Result of the crosses	Symbols used by ANDERSSON-KOTTÖ and GAIRDNER	Difference in chromosome numbers between the species or varietes crossed								n	M
		0	8	15	30	45	60	68	75		
No hybrid was obtained	—	22	—	—	14	—	34	3	3	76	38,0
The F_1 obtained was completely sterile	±	4	—	—	12	—	5	—	1	22	33,4
The F_1 obtained was partly sterile	□	2	—	—	5	—	—	—	2	9	33,3
The F_1 obtained was fertile	○	24	5	1	3	1	2			36	8,6

The authors, commenting on their results, state that »in general it can be said that the success of the cross between species of *Dianthus* depends neither on the systematic position of the species nor on their respective chromosome numbers» (l. c. pp. 86—87). — As the latter part of this statement disagrees with the theory that the degree of quantitative difference between the species crossed is largely responsible for the result of the cross, I have analysed the data, given by these authors, in the same manner as in *Chrysanthemum*. — Though it is obvious that several secondary influences affect the result of a species

cross the data obtained in *Dianthus* nevertheless strikingly confirm my theory.

From Table 4 (p. 331) in the present paper the negative correlation in *Dianthus* between success of the cross and degree of chromosomal difference is obvious. The differences in chromosome number ranged from 0 to 75, eight different values being possible (cf. Table 4). Now, in the category representing negative results of the cross (76 combinations), the average difference in chromosome number between the parents crossed was found to be 38,01. Taking the other extreme, those cases in which the cross succeeded and gave fertile F_1-hybrids, the average chromosomal difference was found to be only 8,62 (36 combinations). The distribution in the two series is obviously different and the difference 38,01—8,62 is no doubt significant. The two other categories representing those crosses, which succeeded but gave more or less sterile F_1-hybrids, seem to be intermediate, having the values 33,41 and 33,33 respectively. — We may thus conclude that *in Dianthus as well as in Chrysanthemum the degree of chromosomal difference largely controls the result of species crosses.*

TABLE 5. *Correlation between chromosomal difference and result of crosses in Viola.* (*Data from* CLAUSEN *1931 b, Tables 1—2.*)

	Difference in chromosome number between the species or varieties crossed																					n	M
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		
Successful crosses	5	2	—	2	3	1	1	1	1	1	1	2	—	—	1	1	—	1					23	5,8
Unsuccessful crosses.....	.	1	2	—	—	1	4	—	1	1	—	—	3	—	—	—	1	—	—	—	1		15	9,2

A similar situation is also met with in *Viola.* CLAUSEN (1931 b) has tabulated the results of species crosses in the *Melanium* section and finds that some combinations are successful, *i. e.* have resulted in F_1-hybrids, while others give negative results. These two categories are summarized in Tables 1 and 2 in the paper cited. In these tables the chromosome numbers of the parents are also given.

I have compared the size of the chromosomal differences in the two categories »successful» and »unsuccessful» crosses. The series obtained are represented in Table 5 in the present paper and were found to be rather different. The average value of the first series is

5,8 as against 9,2 in the second series. It will be observed that the maximum class in the first series is situated at 0, which means that if the types crossed have the same chromosome number the result will be successful. On the other hand, in the second series all combinations were between species with different chromosome number. A calculation by FISHER's χ^2-method (FISHER, 1930) showed that the odds are about 20 : 1 that crosses between species with the same chromosome number give a better result in these cases than crosses between species with different chromosome numbers. — Consequently, also in *Viola* the results accord with our theory.

It has been demonstrated (cf. MÜNTZING, 1933 b) that in numerous other cases crosses between species with the same chromosome number succeed better than crosses between species with different numbers. Thus, it is highly probable that this quantitative control, which has been exemplified by *Chrysanthemum*, *Dianthus* and *Viola*, is a rather widespread phenomenon. It should be expected to occur in all Angiosperm genera having double fertilization and formation of triploid endosperm (MÜNTZING, 1933 b). — The fact that the success of species crosses is largely due to quantitative conditions may also be taken as indirect evidence of the evolutionary significance of quantitative chromosome changes, *i. e.* complete or partial autopolyploidy.

It is obvious, however, that the degree of correlation between quantitative differences and success of the cross is rather different in different genera. It is rather weak in *Viola,* intermediate in *Chrysanthemum* and *Dianthus* and absolute in *Galeopsis.* In this genus only crosses between species with the same chromosome number succeed (MÜNTZING, 1930 a and b). The causes of these differences in behaviour are quite unknown.

Before concluding this discussion on incompatibility among chromosome races and species, it should be emphasized that the occurrence of such barriers of incompatibility and sterility must be very important for the further differentiation of different races by means of secondary processes, such as gene mutations and structural changes. It should also be remembered that intraspecific chromosome races have generally different ecology and geographical distribution. This will also contribute very much to the isolation and independent development of such races. Finally, as emphasized by KOSTOFF and KENDALL (1934, p. 41) the quantitative chromosome change leads to a new kind of organism, which in physiological respects may be rather different from the original diploid type. Therefore, variations and mutations may be expected to

proceed along fairly different lines in the two races. All these circumstances will tend to increase the initial morphological and physiological differences and tend to transform chromosome races, which originally are difficult to distinguish, into clearly different species, which may be distinguished taxonomically without any difficulty.

DARLINGTON (1932, pp. 210—211) thinks that original autopolyploids may in that way be transformed into an allopolyploid condition. This is probable but at present quite hypothetical. — Nevertheless, meiotic studies in some species have demonstrated that the species in question are still in an autopolyploid condition. A number of such cases may be briefly considered.

3. MEIOSIS.

The occurrence of multivalents at meiosis in a number of wild species strongly indicates that they are autopolyploid, though the corresponding diploid forms are not known. Presumably these forms are now extinct, having been replaced by their more sucessful autopolyploid derivatives (compare discussion above, *e. g.* concerning *Biscutella*, p. 289, *Chara* and *Solenobia*, p. 322). — A very good example of this kind is represented by the tetraploid species *Avena elatior* (KATTERMANN, 1931). The somatic chromosome number of this species is 28 and at meiosis 4—7 quadrivalents are present. In spite of the frequent occurrence of quadrivalents the disjunction at I—A was found to be quite regular, 14 chromosomes passing to each pole. — The type of meiosis in this species seems to be very similar to that in *Dactylis glomerata* (cf. above p. 307), but in *Dactylis* the corresponding diploid is known, which is not the case in *Avena elatior*.

Other instances of autopolyploid sexual species which propagate by seeds and in which the corresponding diploid is not known are represented by *Aucuba japonica* (MEURMAN, 1929), *Carex glauca* (HEILBORN, 1932), *Tradescantia reflexa* (ANDERSON and DIEHL, 1932), a *Zauschneria* species (CLAUSEN, KECK and HEUSI, 1934) and a few other cases.

According to the careful investigations of MEURMAN (l. c.), *Aucuba japonica* ($2n = 32$) must be considered to be an autotetraploid, as there are eight different types of somatic chromosomes, which are each represented four times. Further, most of the chromosomes form quadrivalents at meiosis, though other associations also occur. In contrast to *Avena elatior*, chromosome distribution in *Aucuba* was found to be

rather irregular, about 25 per cent of the cells deviating from the normal distribution 16—16.

In *Carex glauca* there is again a frequent occurrence of quadrivalents. HEILBORN (l. c.) observed that the frequency of quadrivalents was highest among the larger chromosomes and considerably lower in the small ones. This is probably due to differences in chiasma frequency. — The somatic chromosome number in this species is 76. If the species is a simple autotetraploid the basic number should be 18. Considering that this value is rather high, it is probable that *Carex glauca*, though in the main an autotetraploid species, may have a more complicated constitution and originally a lower basic number. — *Tradescantia reflexa*, on the contrary, is evidently a typical autotetraploid. The somatic number is 24, the basic number 6. The number of quadrivalents ranged from 1—6 and was on an average 3,4 (ANDERSON and DIEHL, 1932).

The *Zauschneria* species mentioned above was found to be an autotetraploid from two reasons. Firstly, the chromosomes are said to conjugate in »tetrads» instead of in pairs; secondly, it was found by crossing experiments that these chromosomes were capable of complete autosyndesis. — A rather similar situation is met with in *Euchlaena perennis*. According to SHARP (1934, p. 35), quadrivalents are present at meiosis in this species (RANDOLHP, unpubl.) and according to LONGLEY (1924) most of the bivalents present in triploid *Zea* × *Euchlaena perennis* hybrids are formed by autosyndesis of the *Euchlaena* chromosomes. — Another case to be mentioned is the American elm, *Ulmus americana*, which species, according to SAX (1933), is an autotetraploid. However, at meiosis there are no quadrivalents but some indication of secondary association. The absence of true quadrivalents is supposed to be due to the limited chiasma frequency.

The instances given above may suffice to show the similarity in meiotic behaviour between polyploid chromosome races and some polyploid species. — It has been shown above that as regards morphology, ecology and incompatibility intraspecific polyploid chromosome races are characterized by the same essential properties as polyploid species. — This similarity was taken as evidence that polyploid species in many cases should be regarded, either as unchanged autopolyploid chromosome races or as being derived from such races by secondary processes. — *The occurrence of a number of species, in which the mode of meiosis reveals their autopolyploid constitution, demonstrates that new species may really be formed by intraspecific autopolyploidy.* It also de-

monstrates that in some cases the secondary changes, which presumably tend to transform autopolyploidy into allopolyploidy, have not yet been successful.

IV. EVIDENCE FROM AUTOSYNDESIS.

Already in their definition of autopolyploidy, KIHARA and ONO (1927) referred to LJUNGDAHL's case of autosyndesis in *Papaver* (LJUNGDAHL, 1924), which was regarded as conclusive evidence of autopolyploidy. Since then quite a number of similar cases have been reported, which also emphasize the evolutionary significance of autopolyploidy. BLEIER (1934) has tabulated the degree of chromosome pairing and other meiotic characteristics in a large number of hybrids. In some cases reference is also made to the type of syndesis. Out of a total of 119 such hybrids 20 are said to show autosyndesis, 22 to show a mixture of allo- and autosyndesis, the rest being allosyndetic. The proportion of hybrids showing complete or partial autosyndesis is thus rather large and amounts to at least 35 per cent. — The classical cases of autosyndesis, as *e. g.* in *Papaver*, *Digitalis* and *Prunus*, are too well-known to be considered in detail. Some recent typical cases, however, may be discussed below, as they support the conclusions reached by the study of intraspecific chromosome races and by the comparison between intra- and interspecific polyploidy.

In *Chrysanthemum*, SHIMOTOMAI (1931, 1932, 1933) has observed complete or partial autosyndesis in quite a number of hybrids. The meiotic behaviour in these hybrids seems to depend entirely on the chromosome number of the parents. If the difference in chromosome number between the species crossed is an even multiple of the basic number 9 (generally 18) the resulting hybrid will have perfectly regular meiosis with bivalents only. If the numerical difference between the parents is an uneven multiple (generally 9) the supernumerary chromosomes cannot find any mates and appear as univalents at meiosis. A cross 18×36 will consequently give a hybrid with $2n = 54$, which chromosomes form 27 bivalents at meiosis. A cross of the type 18×27, on the contrary, gives an F_1 with $18_{II} + 9_I$ at meiosis. In hybrids of the first kind all gametes receive the same chromosome number and such hybrids therefore behave as new cytologically constant species in contrast to hybrids of the second kind. In *Chrysanthemum* the different genomes are obviously largely homologous and may be recombined at will without serious disturbances. The behaviour of the hybrids seems to depend on purely numerical conditions. Under such circum-

stances, which are quite similar to those found in *Papaver* (LJUNGDAHL, 1924) SHIMOTOMAI's conclusion that most or all of the polyploid *Chrysanthemum* species are autopolyploid cannot be doubted.

In this connection it should be borne in mind that in the discussion above, concerning incompatibility between polyploid species (p. 328), the data from the crossing experiments in *Chrysanthemum* were used to demonstrate the correlation between degree of chromosomal difference and success of the cross. From the close similarity between these crossing results and those found in intraspecific chromosome races and experimental autopolyploids it was concluded that the polyploid species of *Chrysanthemum* (and many other genera) must be mainly autopolyploid. The correctness of this conclusion is evident from the meiotic behaviour in *Chrysanthemum* hybrids, as reported above. — One striking fact, however, remains to be considered. Though the genomes of the polyploid *Chrysanthemum* species are largely homologous, there are no multivalents at meiosis in these species or in balanced hybrids derived from them. In hybrids with univalents, however, a low frequency of multivalents may occur too. The cause of this absence of multivalents is not clear but it may be due to a low chiasma frequency. The absence of multivalents in *Chrysanthemum* reminds one of the meiosis in autotetraploid *Solanum nigrum* (cf. above p. 308) and demonstrates once more that not only those species and races which have multivalents at meiosis are autopolyploid but also other types, which, on account of their meiosis, are now considered to be allopolyploid.

In *Fragaria,* LILIENFELD (1933) has observed a case of autosyndesis which is rather similar to the cases found in *Chrysanthemum.* The cross *F. elatior* ($n = 21$) $\times$ *japonica* ($n = 7$) resulted in F_1-hybrids with 14 bivalents and regular meiosis. This signifies that at least two of the *elatior* genomes are homologous though only bivalents are formed at meiosis in pure *elatior.*

In the genus *Iris,* SIMONET (1934 a and b, 1935) has made some very interesting observations and experiments with regard to autosyndesis. Autosyndetic chromosome conjugation has been observed in five different *Iris* hybrids, involving 6 species. In some cases, representing hybrids between approximately tetraploid and diploid species, the autosyndesis is only partial, the chromosomes of the tetraploid species forming bivalents and those of the diploid species remaining unpaired. Examples of this kind are represented by the following F_1-hybrids: *I. Leichtlinii* ($n = 22$) $\times$ *I. Parib* ($n = 10$) and *I. Korolkowii* ($n = 11$) $\times$ *I. macrantha* ($n = 24$). In the first hybrid there are

$11_{II} + 10_{I}$ at meiosis and in the second $12_{II} + 11_{I}$. The autosyndetic chromosome association in these cases is quite clear not only from the numbers of bivalents and univalents but also from chromosome morphological studies. — Still more interesting, however, are those cases in which there is complete autosyndesis. Three such hybrids have been produced (SIMONET, 1935), the first and most interesting of which is the so-called *Iris autosyndetica*. This type is from the cross *I. Hoogiana* ($n = 22$) $\times$ *I. macrantha* ($n = 24$) and is characterized by perfectly regular meiosis, at which 23 bivalents are formed. The morphology of these bivalents reveals that they are formed by complete autosyndesis, the *macrantha* chromosomes forming twelve and the *Hoogiana* chromosomes eleven bivalents. The new species was found to be self-sterile, but progeny may be obtained from crosses with other similar synthetic types.

These results are rather interesting, firstly because they demonstrate that several *Iris* species are autopolyploid, secondly because they show that constitutional allopolyploids may be synthesized from crosses between different autopolyploids. — As regards the latter point, FAGERLIND (1934), in connection with his cytological results in *Galium*, has briefly discussed this possibility. Crosses between two autotetraploids *MMMM* and *VVVV* would give an F_1-hybrid *MMVV*. In case of autosyndesis this F_1-hybrid would behave as a new constant allopolyploid. This case has evidently already been realized in *Iris*. The parent species of *Iris autosyndetica* are rather distantly related and belong to different sections of the genus. Both as regards the intermediate morphological characters and the regular meiosis this synthetic type behaves as a typical allopolyploid, though it arose from two autopolyploids. — Consequently, *the importance of autopolyploidy is not limited to the production of new gigas types with new physiological qualities but also includes the formation of new allopolyploids by means of crosses between different autopolyploids.*

The hybrid *Crepis setosa* $\times$ *biennis* (COLLINS and MANN, 1923) has furnished one of the best known examples of autosyndesis. The study of this hybrid and its derivatives has demonstrated that the 20 haploid chromosomes of *C. biennis* consist of four genomes of five chromosomes, each genome being capable of forming bivalents with the other genomes. On account of these results *C. biennis* has generally been looked upon as a good example of an autopolyploid species. BABCOCK and SWEZY (1935), however, have taken up this question again and have reached somewhat divergent conclusions. These authors find

that in *C. biennis* there are 10 types of chromosomes, which are probably present four times. The 10 types fall into 5 groups, each with 2 rather similar chromosomes, but the members of these pairs of chromosomes seem to be slightly different. The authors therefore conclude that *biennis* has probably arisen by hybridization between two 5-paired closely related species or subspecies followed by doubling, thus producing a 10-paired allopolyploid species, and this succeeded by a second doubling. If that is the case, and not all the eight genomes are structurally alike, *C. biennis* should be considered as an allooctoploid, although its chromosome behaviour in hybrids is essentially that of an autooctoploid (l. c. p. 261). In spite of these terminological difficulties, however, it is evident that the most important process in the genesis of this species has been the repeated doubling of the chromosomes. Thanks to this process the species is more characterized by the quantitative increase in chromosome number and the homology of several genomes than by the slight structural differences which occur. Further, it is not excluded, as the authors point out, that the structural changes may be of secondary origin, having changed an original autooctoploid in an allooctoploid direction. This possibility gains some support from the study of another octoploid species, *Crepis ciliata.* The chromosomes of this species were analysed in the same way as in *C. biennis.* Ten types of chromosomes could again be distinguished, and these could be grouped into 5 pairs. The members of each pair were found on an average to be still more similar than in *C. biennis* and, consequently, *C. ciliata* is probably a true autopolyploid or very near this condition.

Finally, it should be mentioned that the probable absence of quadrivalents in *C. biennis* cannot be taken as evidence of allopolyploidy, since experimental autopolyploids are known, which have regular meiosis practically without multivalents (*Solanum nigrum*, cf. above p. 308). The same objection may be raised against the inference (l. c. p. 263) that the absence of quadrivalents in LJUNGDAHL's *Papaver* hybrids indicates allopolyploidy. The *Papaver* species, more probably, may be compared to the autopolyploid *Chrysanthemum* species. As reported above these species have no multivalents at meiosis in spite of their clearly autopolyploid condition.

Besides the typical instances of autosyndesis discussed above, which indicate complete or almost complete autopolyploidy, many other cases are known (cf. BLEIER, 1934) in which autosyndesis may be only partial. There seem to be continuous transitions between the cases of complete autosyndesis and such cases in which this phenomenon ceases

to be apparent. — Judging from recent investigations, it seems as if the different genomes in polyploid species, even in species which are regarded as typically allopolyploid, such as *e. g. Triticum vulgare* and *Phleum pratense*, are seldom completely differentiated. Very often partial homology is evident from the occurrence of unexpected associations at meiosis of two or more chromosomes. This may occur in certain hybrids, in which the different genomes are single and in which the chromosomes therefore cannot pair with their usual homologues. Instead of that they have an opportunity of associating with completely or partially homologous chromosomes belonging to other genomes. — Typical cases of such partial autosyndesis have been studied, for instance, in wheat hybrids by KIHARA and his school (cf. KIHARA and NISHIYAMA, 1930; KIHARA and LILIENFELD, 1932) and by KATTERMANN (1934).

Though such cases of partial autosyndesis may be shown by species which are undoubtedly allopolyploid, the conjugation of chromosomes belonging to different genomes nevertheless demonstrates that during the phylesis of such species reduplication of certain chromosomes or at least parts of chromosomes has occurred. This signifies a quantitative increase of chromatin, which in principle is of the same kind as in cases of strict autopolyploidy. The only difference is that in the first case the increase is partial, in the latter case total. *The numerous cases of autosyndesis in hybrids consequently emphasize the evolutionary significance of quantitative chromosome increase.* Such an increase has chiefly occurred in autopolyploids but to a considerable extent also in allopolyploids (cf. below, p. 361).

V. COMPARISON BETWEEN THE CHROMOSOME NUMBERS OF ANNUAL AND PERENNIAL SPECIES.

In a preceding chapter (p. 293), dealing with the physiological consequences of chromosome doubling, it was demonstrated that experimental autopolyploids are generally characterized by a retarded rate of growth, probably caused by a slowing down of the rate of cell division. This retardation was found to be characteristic also of several polyploid chromosome races, both in plants and animals. — As a working hypothesis it was assumed that the rate of growth might also influence the type of life form, since it is known that perennial species in contrast to annual species need a much longer time for their full development. Perennial species seldom flower the first year after ger-

mination and as a rule require several years to reach their maximum size. If this difference in growth rhythm is correlated with the rate of cell division a positive correlation between chromosome number and perennial habit of life might be expected.

This possibility is very much strengthened by the fact that, according to SHARP (1934, p. 342), the autotetraploid *Zea* race, experimentally produced by RANDOLPH, was found to be perennial in contrast to the ordinary diploid maize, which is annual. — Similar conditions also prevail in some of the wild chromosome races discussed above. The polyploid *Nasturtium* biotypes were found to be slower in development than the diploid race and had also a tendency to be perennial (cf. p. 299). The tetraploid gigas type in *Allium Schoenoprasum* is also slow in development and does not reach its full size so quickly as the diploids (cf. p. 299). Further, with regard to *Eragrostis,* HAGERUP (1931) reports that the type with the lowest chromosome number is a short-lived annual, the polyploid races, on the contrary, being perennial (cf. p. 290).

Some other similar cases, not taken from intraspecific chromosome races but from different species of a genus, are also described in the literature. Of the two *Euchlaena* species, *E. mexicana* is diploid and annual, *E. perennis* tetraploid and perennial (LONGLEY, 1924). As mentioned above (p. 335) the latter species is probably autotetraploid, having quadrivalents at meiosis, and being capable of autosyndesis in certain crosses. — Correlation between chromosome number and duration of life has also been observed by LONGLEY (1932) in the genus *Sorghum*. Two of the species in this genus, *S. sudanensis* and *halepense*, are hardly distinguishable except that the former has $n = 10$ and is annual, the latter $n = 20$ and perennial. HUSKINS and SMITH (1932) also report that *halepense* is perennial in contrast to all other *Sorghum* species with half the chromosome number of *halepense*. According to LONGLEY (l. c.), the genus also comprises a species with $n = 5$, *S. versicolor*, and this was found to be a short-lived annual with a more shortened span of life than any of the other species. However, the correlation in the genus between chromosome number and perennial habit is weakened by the fact that another annual species, *purpureo-sericeum*, was found to have $n = 20$, like the only perennial species, *S. halepense*.

Among the pseudogamous *Potentilla* species, studied by the present writer (cf. MÜNTZING, 1931 a), all species and biotypes are strictly perennial with the exception of two *argentea* biotypes (*A*—*A* and *A*—*G*), which are annual or subperennial. These biotypes are diploid ($2n = 14$).

All hexaploid and octoploid *argentea* biotypes, represented in the material, are perennial. — A similar state of things is found in *Taraxacum*. Dr. Å. GUSTAFSSON has kindly informed me that the only biennial *Taraxacum* type known is diploid, in contrast to the perennial species and biotypes, which are generally polyploid. — Finally, according to Dr. E. SÖDERBERG (verbal information), correlation between chromosome number and rate of development also prevails in the genus *Nymphaea*. In this genus, which has been studied cytologically by LANGLET and SÖDERBERG (1927), *N. stellata* (2n = 28) flowers 12 weeks after the sowing. *N. rubra* and *N. lotus* (2n = 56) are slower and do not flower until 15—16 weeks after sowing and *N. gigantea* (2n = 224) requires more than a year to reach this state of development. — This beautiful correlation, however, is somewhat disturbed by the fact that the Swedish *Nymphaea* species do not flower until the third year after sowing, though their chromosome numbers are lower than those in *gigantea* but higher than those in the other species mentioned. According to LANGLET and SÖDERBERG (l. c.), *N. alba* has 2n = 64, *N. candida* 2n = about 112.

On account of all the facts enumerated above, which indicate a connection between chromosome number and type of life form, I decided to make a statistical study of this problem on the basis of as large a material as possible. As a preliminary test, in which the Scandinavian Angiosperm species were employed, gave evidence of positive correlation, the work was extended to include 48 genera, comprising 582 species. — The data were gathered in the following way: With the aid of the floristical text-books of GARCKE (1895) and SCHINZ and KELLER (1909) on the flora of Germany and Switzerland all genera comprising species with different life forms were noted. During this work the Scandinavian flora was also considered, thanks to verbal information from Dr. N. SYLVÉN and comparison with different Swedish textbooks. — The chromosome numbers of the species in these genera were chiefly looked for in the following chromosome lists: GAISER (1926, 1930 a, 1930 b, 1933), TISCHLER (1931) and AVDULOW (1931). Additional data were gathered from WANSCHER (1931, 1932, 1933), SIMONET (1934 b), HOFELICH (1935), GRAZE (1935), HOLLINGSHEAD and BABCOCK (1930), BABCOCK and CAMERON (1934), AFZELIUS (1924), BRUUN (1932), FAGERLIND (1934), CLAUSEN (1931 b) and PETERSON (1935).

Many genera had to be excluded from further study on account of insufficient data as to the chromosome numbers. In each of 48 genera, however, the chromosome numbers were known for at least two and

generally several species, having different life forms. — As the chromosome lists often contained the chromosome numbers of other species than those occurring in Scandinavia and Middle Europe, the names of such species in the 48 genera studied were recorded. Thanks to valuable assistance given by Dr. A. HÄSSLER of the Botanical Museum at Lund, I received information as to the life forms of most of these species. During his work Dr. HÄSSLER used a series of different botanical works, chiefly DE CANDOLLE's »Prodromus systematis naturalis regni vegetabilis». The number of species studied was in this way increased from about 450 to 582.

From the preceding it is evident that the data gathered represent a random sample, which is large enough to allow rather definite conclusions. I am aware that owing to different sources of error (chiefly questions of nomenclature) the information gathered may not be correct in all details, but the errors possibly present cannot disturb the main conclusions to be drawn from Tables 6—7 (pp. 351—353) and Diagram 1 (p. 354). — For control I have found it necessary to publish the following enumeration of the names of all species studied and their respective haploid chromosome numbers. In each genus the species are grouped in three categories 1) annual, 2) biennial or subperennial and 3) perennial species. In many genera only two of these categories are represented. Below each genus the average chromosome numbers of each category are given (M_a = average of annual, M_b of biennial and M_p of perennial species; n_a, n_b and n_p = the corresponding number of species).

The following genera and species were studied:

Helianthus

Annual species: *annuus* (17).
Perennial species: *tuberosus* (51).
$M_a = 17{,}0$; $M_p = 51{,}0$ $n_a = 1$; $n_p = 1$

Senecio

Annual species: *discifolius* (5), *elegans* (10), *glutinosus* (10), *silvaticus* (20), *vernalis* (10), *viscosus* (20), *vulgaris* (20).
Biennial or subperennial species: *nebrodensis* (10), *paluster* (24).
Perennial species: *abrotanifolius* (20), *alpestris* (23—25), *erucifolius* (20), *fluviatilis* (20), *Fuchsii* (20), *Heritieri* (30), *Jacobaea* (20), *paludosus* (20) *Petasites* (30), *Roberti-Friesii* (± 90), *subalpinus* (20).
$M_a = 13{,}6$; $M_b = 17{,}0$; $M_p = 28{,}5$ $n_a = 7$; $n_b = 2$; $n_p = 11$

Crepis, Subgenus *Catonia*

Perennial species: *alpestris* (4), *aurea* (5), *bhotanica* (8), *blattaroides* (4), *bungei* (4), *burejensis* (4), *chrysantha* (4), *conyzaefolia* (4), *crocea* (8), *hookeriana*

(4), *hypochaeridea* (4), *kashmirica* (6), *paludosa* (6), *polytrica* (8), *pontana* (5), *sibirica* (5), *viscidula* (6).

$M_p = 5{,}2$ $n_p = 17$

Crepis, Subgenus *Eucrepis*

Annual species: *argolica* (4), *bifida* (5), *capillaris* (3), *dioscoridis* (4), *gracilis* (11, 55/2), *granatensis* (4), *multiflora* (4), *neglecta* (3, 4), *palaestina* (4), *parviflora* (4), *pterothecoides* (4), *pulchra* (4), *sancta* (5), *stojanovii* (4), *suberostris* (5), *suffreniana* (4), *tectorum* (4), *tubaeformis* (4).

Biennial or subperennial species: *biennis* (20), *ciliata* (20), *nicaeensis* (4).

Perennial species: *acuminata* (33/2, 22, 55/2), *Andersonii* (11), *bithynica* (5), *chondrilloides* (4), *eigiana* (4), *elegans* (7), *flexuosa* (7), *glauca* (11), *gymnopus* (4), *incarnata* (4), *lacera* (4), *nana* (7), *occidentalis* (11, 22), *oreades* (4), *pannonica* (4), *praemorsa* (4), *raulina* (5), *reuteriana* (4), *robertoides* (4), *runcinata* (11).

$M_a = 4{,}9$; $M_b = 14{,}7$; $M_p = 7{,}1$ $n_a = 18$; $n_b = 3$; $n_p = 20$

Crepis, Subgenus *Barkhausia*

Annual species: *aculeata* (4), *alpina* (5), *amplexifolia* (4), *aspera* (4), *Bureniana* (4), *foetida* (5), *juvenalis* (4), *nigricans* (4), *rubra* (5), *senecioides* (4), *setosa* (4).

Perennial species: *albida* (5), *bellidifolia* (4), *bursifolia* (4), *canariensis* (4), *clausonis* (4), *divaricata* (4), *fontiana* (4), *hieracioides* (4), *hyemalis* (4), *triasii* (4).

$M_a = 4{,}3$; $M_p = 4{,}1$ $n_a = 11$; $n_p = 10$

Lactuca

Annual species: *sativa* (9).

Biennial or subperennial species: *scariola* (9), *virosa* (8).

Perennial species: *muralis* (9), *perennis* (8)

$M_a = 9{,}0$; $M_b = 8{,}5$; $M_p = 8{,}5$ $n_a = 1$; $n_b = 2$; $n_p = 2$

Galium

Annual species: *aparine* (33, 44), *parisiense* (11, 22, 33), *saccharatum* (11), *spurium* (10), *Vaillantii* (10).

Perennial species: *anisophyllum* (22), *aristatum* (22), *boreale* (22, 33), *cruciatum* (11), *helveticum* (33), *mollugo* (11, 22, 33), *ochroleucum* (22), *palustre* (12, 48), *rubioides* (66), *saxatile* (22), *Schultesii* (33), *trifidum* (12), *uliginosum* (11, 22), *vernum* (22), *verum* (11, 22, 33).

$M_a = 18{,}3$; $M_p = 25{,}5$ $n_a = 5$; $n_p = 15$

Myosotis

Annual species: *intermedia* (24).

Perennial species: *palustris* (32).

$M_a = 24{,}0$; $M_p = 32{,}0$ $n_a = 1$; $n_p = 1$

Lamium

Annual species: *amplexicaule* (9), *dissectum* (18), *intermedium* (18), *purpureum* (9).

Perennial species: *album* (9), *galeobdolon* (18), *maculatum* (9).

$M_a = 13{,}5$; $M_p = 12{,}0$ $n_a = 4$; $n_p = 3$

Salvia

Annual species: *hispanica* (6), *lanceolata* (10), *viridis* (8).
Biennial or subperennial species: *argentea* (10), *hirsuta* (11), *Sclarea* (11).
Perennial species: *azurea* (10), *carduacea* (16), *glutinosa* (8), *hians* (16), *nutans* (8), *officinalis* (8), *patens* (9), *pratensis* (16), *pseudococcinea* (11?), *recognita* (7), *ringens* (6), *silvestris* (8), *splendens* (22), *tiliaefolia* (11), *verticillata* (8).
$M_a = 8{,}0$; $M_b = 10{,}7$; $M_p = 10{,}9$ $n_a = 3$; $n_b = 3$; $n_p = 15$

Solanum

Annual species: *alatum* (24), *nigrum* (36), *villosum* (24).
Perennial species: *dulcamara* (36).
$M_a = 28{,}0$; $M_p = 36{,}0$ $n_a = 3$; $n_p = 1$

Verbascum

Biennial or subperennial species: *Blattaria* (15, 16), *lychnitis* (16), *maurum* (32), *montanum* (16), *phlomoides* (16), *phoenicium* (16), *pulverulentum* (16), *Ternacha* (24), *thapsiforme* (16), *thapsus* (17—18).
Perennial species: *chaixii* (about 16), *nigrum* (15), *pyramidatum* (16).
$M_b = 18{,}5$; $M_p = 15{,}7$ $n_b = 10$; $n_p = 3$

Digitalis

Biennial or subperennial species: *purpurea* (28).
Perennial species: *ambigua* (28), *canariensis* (28), *lutea* (48), *viridiflora* (28).
$M_b = 28{,}0$; $M_p = 33{,}0$ $n_b = 1$; $n_p = 4$

Linaria

Annual species: *alpina* (6), *arvensis* (6), *chalepensis* (12), *Pancicii* (8).
Perennial species: *genistifolia* (6), *repens* (6), *striata* (6), *supina* (6), *vulgaris* (6).
$M_a = 8{,}0$; $M_p = 6{,}0$ $n_a = 4$; $n_p = 5$

Veronica

Annual species: *acinifolia* (7), *arvensis* (8), *hederifolia* (28), *opaca* (12, 14), *polita* (7), *praecox* (9), *Tournefortii* (14), *triphyllos* (7), *verna* (8).
Perennial species: *beccabunga* (9), *chamaedrys* (16), *fruticans* (8), *gentianoides* (24), *longifolia* (34, 36), *maritima* (17), *montana* (9), *officinalis* (16, 18), *orchidea* (17), *prostrata* (16), *serpyllifolia* (7), *spicata* (32), *spuria* (17), *teucrium* (32).
$M_a = 11{,}2$; $M_p = 18{,}3$ $n_a = 9$; $n_p = 14$

Ranunculus

Annual species: *arvensis* (16), *ophioglossifolius* (8), *sardous* (8), *trilobus* (24).
Perennial species: *acer* (7, 14), *aconitifolius* (8), *alpester* (8), *auricomus* (16, 24), *bulbosus* (8), *cassubicus* (16), *flammula* (16), *glacialis* (8), *hederaceus* (8), *illyricus* (16), *lanuginosus* (7, 14), *lingua* (64), *montanus* (8), *nemorosus* (8), *platanifolius* (7), *pyrenaeus* (16), *repens* (8, 16), *reptans* (16), *Villarsii* (7).
$M_a = 14{,}0$; $M_p = 14{,}1$ $n_a = 4$; $n_p = 19$

Adonis

Annual species: *aestivalis* (16), *autumnalis* (16), *flammeus* (16).
Perennial species: *pyrenaica* (8), *vernalis* (8, 12).
$M_a = 16{,}0$; $M_p = 9{,}0$ $n_a = 3$; $n_p = 2$

Papaver

Annual species: *dubium* (14), *hybridum* (7), *Rhoeas* (7), *somniferum* (11).
Perennial species: *alpinum* (7), *nudicaule* (7, 35), *radicatum* (35).
$M_a = 9{,}8$; $M_p = 21{,}0$ $n_a = 4$; $n_p = 3$

Erysimum

Annual species: *cheiranthoides* (8), *Perowskianum* (18), *repandum* (8).
Biennial or subperennial species: *canescens* (36), *cuspidatum* (8), *thyrsoideum* (8).
Perennial species: *helveticum* (24), *hieraciefolium* (16), *linifolium* (7), *ochroleucum* (about 16), *purpureum* (24), *rupestre* (32), *silvestre* (about 24).
$M_a = 11{,}3$; $M_b = 17{,}3$; $M_p = 20{,}4$ $n_a = 3$; $n_b = 3$; $n_p = 7$

Sisymbrium

Annual species: *altissimum* (7), *Irio* (7), *Loeselii* (7), *runcinatum* (21), *Sophia* (14), *supinum* (16).
Biennial or subperennial species: *austriacum* (7), *orientale* (7).
Perennial species: *strictissimum* (14).
$M_a = 12{,}0$; $M_b = 7{,}0$; $M_p = 14{,}0$ $n_a = 6$; $n_b = 2$; $n_p = 1$

Cardamine

Annual species: *graeca* (8).
Biennial or subperennial species: *flexuosa* (16), *hirsuta* (8), *impatiens* (8), *Plumieri* (about 20).
Perennial species: *alpina* (8), *amara* (8), *asarifolia* (8), *californica* (16), *pratensis* (16, 32), *resedifolia* (8), *trifolia* (8).
$M_a = 8{,}0$; $M_b = 13{,}0$; $M_p = 11{,}4$ $n_a = 1$; $n_b = 4$; $n_p = 7$

Lepidium

Annual species: *perfoliatum* (8), *ruderale* (16), *sativum* (8), *virginianum* (16).
Biennial or subperennial species: *densiflorum* (16), *graminifolium* (8).
Perennial species: *amplexicaule* (20), *Draba* (32), *latifolium* (12).
$M_a = 12{,}0$; $M_b = 12{,}0$; $M_p = 21{,}3$ $n_a = 4$; $n_b = 2$; $n_p = 3$

Thlaspi

Annual species: *arvense* (7).
Perennial species: *alpestre* (7), *montanum* (14), *rotundifolium* (7).
$M_a = 7{,}0$; $M_p = 9{,}3$ $n_a = 1$; $n_p = 3$

Alyssum

Annual species: *calycinum* (16), *campestre* (8), *dasycarpum* (8), *linifolium* (8), *rostratum* (8).
Biennial or subperennial species: *edentulum* (8).
Perennial species: *Arduinii* (8), *argenteum* (8), *corymbosum* (8), *creticum* (8), *floribundum* (8), *leucadum* (8), *montanum* (8), *murale* (8), *orientale* (8), *ovirense* (8), *pyrenaicum* (16), *spinosum* (16), *tortuosum* (8).
$M_a = 9{,}6$; $M_b = 8{,}0$; $M_p = 9{,}2$ $n_a = 5$; $n_b = 8$; $n_p = 13$

Linum

Annual species: *catharticum* (8), *strictum* (9), *usitatissimum* (15).
Perennial species: *alpinum* (18), *altaicum* (9), *angustifolium* (15—16), *austriacum*

(9), *campanulatum* (14), *capitatum* (12), *corymbiferum* (15), *flavum* (15), *hologynum* (9), *Lewisii* (9), *maritimum* (10), *monogynum* (43?), *narbonense* (9), *nervosum* (15), *perenne* (9), *punctatum* (9), *salsoloides* (9), *sibiricum* (9).

$M_a = 10{,}7$; $M_p = 13{,}3$ $n_a = 3$; $n_p = 18$

Viola (*Tricolores*)

Annual species: *arvensis* (17), *diffusa* (13), *Kitaibeliana* (7, 18, 24), *tricolor* (13).

Biennial or subperennial species: *elegantula* (10), *Orphanidis* (11), *tricolor* (13).

Perennial species: *Battandierii* (26—30), *cornuta* (11), *lutea* (24), *rotomagensis* (17), *tricolor* (13).

$M_a = 14{,}8$; $M_b = 11{,}3$; $M_p = 18{,}6$ $n_a = 4$; $n_b = 3$; $n_p = 5$

Mercurialis

Annual species: *annua* (8).

Perennial species: *leiocarpa* (24), *perennis* (>32).

$M_a = 8{,}0$; $M_p = 28{,}0$ $n_a = 1$; $n_p = 2$

Urtica

Annual species: *Dodarti* (12), *pilulifera* (12), *urens* (12).

Perennial species: *dioica* (24).

$M_a = 12{,}0$; $M_p = 24{,}0$ $n_a = 3$; $n_p = 1$

Polygonum

Annual species: *argyrocoleon* (20), *aviculare* (20), *Bellardi* (10), *convolvulus* (10), *danubiale* (11), *dumetorum* (10), *hydropiper* (10), *lapathifolium* (11), *nodosum* (11), *persicaria* (22), *plebejum* (20), *tinctorum* (20), *tomentosum* (11).

Perennial species: *alpinum* (10), *ambiguum* (22), *amphibium* (about 33), *bistorta* (22), *cuspidatum* (44), *divaricatum* (55), *sachalinense* (22), *spectabile* (33), *virginianum* (22), *viviparum* (55).

$M_a = 14{,}3$; $M_p = 31{,}8$ $n_a = 13$; $n_p = 10$

Rumex

Biennial or subperennial species: *limosus* (20), *maritimus* (20), *pulcher* (10, 20).

Perennial species: *acetosa* (7, 8), *acetosella* (21), *alpinus* (10), *aquaticus* (about 100), *arifolius* (7, 8), *conglomeratus* (10), *crispus* (30), *domesticus* (20, 30, 40), *hydrolapathum* (100), *hymenosepalus* (50), *japonicus* (50), *nivalis* (7, 8), *obtusifolius* (20), *orientalis* (30), *patientia* (30), *sanguineus* (10), *scutatus* (10).

$M_b = 18{,}3$; $M_p = 30{,}8$ $n_b = 3$; $n_p = 17$

Silene

Annual species: *armeria* (12), *conica* (12), *conoidea* (12), *cretica* (12), *dichotoma* (12), *gallica* (12), *linicola* (12), *noctiflora* (12).

Perennial species: *acaulis* (12), *ciliata* (12, 24, 96), *inflata* (12), *italica* (12), *longiflora* (12), *nutans* (12), *Otites* (12), *rupestris* (12), *saxifraga* (12), *tatarica* (12), *vallesia* (12, 24).

$M_a = 12{,}0$; $M_p = 15{,}5$ $n_a = 8$; $n_p = 11$

Stellaria

Annual species: *apetala* (11), *media* (22), *neglecta* (11, 22).

Perennial species: *crassifolia* (13), *graminea* (13—14), *holostea* (10, 13), *longi-*

folia (13), *nemorum* (13), *palustris* (>50), *ruscifolia* (about 25), *uliginosum* (12—13).

$M_a = 16{,}5$; $M_p = 18{,}9$ $n_a = 3$; $n_p = 8$

Chenopodium

Annual species: *album* (9), *hybridum* (9), *murale* (9), *vulvaria* (9).
Perennial species: *Bonus Henricus* (18).
$M_a = 9{,}0$; $M_p = 18{,}0$ $n_a = 4$; $n_p = 1$

Beta

Biennial or subperennial species: *maritima* (9).
Perennial species: *trigyna* (27).
$M_b = 9{,}0$; $M_p = 27{,}0$ $n_b = 1$; $n_p = 1$

Vicia

Annual species: *angustifolia* (5, 6) *dasycarpa* (7), *Ervilia* (7), *Faba* (6), *gracilis* (7), *hirsuta* (7), *hybrida* (6), *lathyroides* (5, 7), *lutea* (7), *monanthos* (7), *narbonensis* (7), *pannonica* (6), *peregrina* (7), *sativa* (6, 7), *tetrasperma* (7).
Perennial species: *cracca* (6, 7, 14), *orobus* (6), *sepium* (7), *silvatica* (7), *tenuifolia* (12), *unijuga* (6, 12, 18), *villosa* (7).
$M_a = 6{,}6$; $M_p = 8{,}6$ $n_a = 15$; $n_p = 7$

Medicago

Annual species: *apiculata* (8), *arabica* (8), *denticulata* (7, 8), *Gerardi* (8), *hispida* (7), *maculata* (8), *minima* (8), *nigra* (7, 8), *rigidula* (8), *rugosa* (16), *scutellata* (16), *terebellum* (7).
Biennial or subperennial species: *lupulina* (8, 16).
Perennial species: *arborea* (16), *falcata* (16), *sativa* (16).
$M_a = 9{,}1$; $M_b = 12{,}0$; $M_p = 16{,}0$ $n_a = 12$; $n_b = 2$; $n_p = 3$

Trifolium

Annual species: *arvense* (7), *campestre* (7), *filiforme* (7), *incarnatum* (7, 8), *minus* (14), *parviflorum* (8), *procumbens* (7), *scabrum* (8), *spadiceum* (7).
Biennial or subperennial species: *hybridum* (8), *pratense* (7).
Perennial species: *alpestre* (8), *fragiferum* (8), *lupinaster* (24), *medium* (40, 49), *montanum* (9), *ochroleucum* (8), *pannonicum* (90), *repens* (16), *rubens* (8), *Thalii* (8).
$M_a = 8{,}1$; $M_b = 7{,}5$; $M_p = 22{,}4$ $n_a = 9$; $n_b = 2$; $n_p = 10$

Anthriscus

Annual species: *cerefolium* (9), *vulgaris* (9).
Perennial species: *silvestris* (8).
$M_a = 9{,}0$; $M_p = 8{,}0$ $n_a = 2$; $n_p = 1$

Carum

Biennial or subperennial species: *carvi* (10, 11).
Perennial species: *Bulbocastanum* (11).
$M_b = 10{,}5$; $M_p = 11{,}0$ $n_b = 1$; $n_p = 1$

Bupleurum

Annual species: *rotundifolium* (8), *tenuissimum* (8).
Perennial species: *longifolium* (8).
$M_a = 8{,}0$; $M_p = 8{,}0$ $n_a = 2$; $n_p = 1$

Alopecurus

Annual species: *agrestis* (7), *fulvus* (7), *myosuroides* (7).
Biennial or subperennial species: *geniculatus* (14).
Perennial species: *antarcticus* (>50), *pratensis* (14).
$M_a = 7{,}0$; $M_b = 14{,}0$; $M_p = 32{,}0$ $n_a = 3$; $n_b = 1$; $n_p = 2$

Phleum

Annual species: *asperum* (14).
Perennial species: *alpinum* (7, 14), *ambiguum* (14), *Boehmeri* (7), *Michaeli* (7), *nodosum* (7), *pratense* (21).
$M_a = 14{,}0$; $M_p = 11{,}1$ $n_a = 1$; $n_p = 6$

Phalaris

Annual species: *canariensis* (6), *minor* (14).
Perennial species: *arundinacea* (7, 14).
$M_a = 10{,}0$; $M_p = 10{,}5$ $n_a = 2$; $n_p = 1$

Anthoxanthum

Annual species: *aristatum* (5).
Perennial species: *odoratum* (10).
$M_a = 5{,}0$; $M_p = 10{,}0$ $n_a = 1$; $n_p = 1$

Hordeum

Annual species: *caput medusae* (7), *jubatum* (14), *maritimum* (7), *murinum* (7, 14), *spontaneum* (7).
Perennial species: *bulbosum* (14), *nodosum* (7, 21), *secalinum* (7, 14), *silvaticum* (14).
$M_a = 9{,}1$; $M_p = 13{,}1$ $n_a = 5$; $n_p = 4$

Lolium

Annual species: *multiflorum* (7), *remotum* (7), *temulentum* (7).
Perennial species: *perenne* (7).
$M_a = 7{,}0$; $M_p = 7{,}0$ $n_a = 3$; $n_p = 1$

Festuca

Annual species: *myuros* (7, 21), *rigida* (7), *sciuroides* (7).
Perennial species: *amethystina* (14), *arundinacea* (14, 21, 35), *duriuscula* (21), *gigantea* (21), *maritima* (7), *ovina* (7, 14, 21, 35), *pratensis* (7, 14), *pulchella* (7), *rubra* (7, 21, 28, 35), *silvatica* (21), *varia* (7, 14, 21).
$M_a = 9{,}3$; $M_p = 16{,}2$ $n_a = 3$; $n_p = 11$

Bromus

Annual species: *arduennensis* (7), *arvensis* (7), *japonicus* (7), *madritensis* (21), *mollis* (14), *patulus* (7), *secalinus* (14), *squarrosus* (7), *sterilis* (7), *tectorum* (7), *uniloides* (14).
Biennial or subperennial species: *breviaristatus* (28), *maximus* (28).

Perennial species: *cappadocicus* (21), *carinatus* (28), *erectus* (21), *inermis* (21, 28), *pacificus* (21), *polyanthus* (21), *pumpellianus* (21), *ramosus* (7), *sitchensis* (21), *variegatus* (21).

$M_a = 10{,}2$; $M_b = 28{,}0$; $M_p = 20.7$ $n_a = 11$; $n_b = 2$; $n_p = 10$

Poa

Annual species: *annua* (14).

Perennial species: *alpina* (21), *angustifolia* (14, 28, 35), *caesia* (21), *compressa* (21, 28), *glauca* (35), *nemoralis* (14, 21), *palustris* (14, 21), *pratensis* (25—42), *sudetica* (7), *trivialis* (7), *violacea* (14).

$M_a = 14{,}0$; $M_p = 20{,}5$ $n_a = 1$; $n_p = 11$

Avena

Annual species: *fatua* (21), *sativa* (21), *strigosa* (7).

Perennial species: *pubescens* (14), (*Arrhenatherum*) *elatius* (14), (*Trisetum*) *flavescens* (24), (*Trisetum*) *sibiricum* (14).

$M_a = 16{,}3$; $M_p = 16{,}5$ $n_a = 3$; $n_p = 4$

The average values obtained from the different genera are summarized in Table 6 (pp. 351—352). Of special interest in this table are the differences M_p—M_a, M_p—M_b and M_b—M_a. Considering first M_p—M_a, it is striking that this difference has almost always a positive value. In other words, *the perennial species in a genus have in most cases a higher average chromosome number than the annual species of the same genus.* This conclusion is statistically significant. Of 44 genera, in which the chromosome numbers of annual as well as perennial species are known, 34 were found to give positive M_p—M_a values, 8 gave negative values and in 2 genera the difference was ± 0. Considering only the + and — differences, the expected distribution if no correlation were present would be $21 : 21 \pm 3{,}24$. The difference found is 13,00 and $D/m_D = 4{,}01$. — As the *relation* between the M_p and M_a values might be more instructive than the numerical difference, the values $M_p : M_a$ have been calculated and included in Table 6. These values range from 0,6 to 4,6. 32 genera have values higher than 1,0, as compared to 6 genera in which the values are below 1,0.

The other differences calculated are too few to be statistically significant but go in the same direction. M_p—M_b values are available in 19 genera and were found to be positive in 14 cases, negative in 4 cases and ± 0 in one genus. The D/m_D value in this case will be 2,38, the odds consequently being 57 to 1 that the perennial species in the material studied have higher chromosome numbers than the biennial or subperennial species. — The difference M_b—M_a, finally, is represented in 14 genera and has positive values in 8 cases, negative values in 5 cases and is ± 0 in one case.

TABLE 6. *The average chromosome numbers of annual, biennial and perennial species in 48 genera.*

Genus	Annual species		Biennial or subperennial species		Perennial species		Differences			M_p/M_a
	n	M	n	M	n	M	M_p-M_a	M_p-M_b	M_b-M_a	
Helianthus	1	17,0	—	—	1	51,0	+ 34,0	—	—	3,0
Senecio	7	13,6	2	17,0	11	28,5	+ 14,9	+ 11,5	+ 3,4	2,1
Crepis; Subgenus *Catonia*	—	—	—	—	17	5,2	—	—	—	—
Crepis; Subgenus *Eucrepis*	18	4,9	3	14,7	20	7,1	+ 2,2	— 7,6	+ 9,8	1,5
Crepis; Subgenus *Barkhausia*	11	4,3	—	—	10	4,1	— 0,2	—	—	0,95
Lactuca	1	9,0	2	8,5	2	8,5	— 0,5	± 0,0	— 0,5	0,9
Galium	5	18,3	—	—	15	25,5	+ 7,2	—	—	1,4
Myosotis	1	24,0	—	—	1	32,0	+ 8,0	—	—	1,3
Lamium	4	13,5	—	—	3	12,0	— 1,5	—	—	0,9
Salvia	3	8,0	3	10,7	15	10,9	+ 2,9	+ 0,2	+ 2,7	1,4
Solanum	3	28,0	—	—	1	36,0	+ 8,0	—	—	1,3
Verbascum	—	—	10	18,5	3	15,7	—	— 2,8	—	—
Digitalis	—	—	1	28,0	4	33,0	—	+ 5,0	—	—
Linaria	4	8,0	—	—	5	6,0	— 2,0	—	—	0,75
Veronica	9	11,2	—	—	14	18,3	+ 7,1	—	—	1,6
Ranunculus	4	14,0	—	—	19	14,1	+ 0,1	—	—	1,0
Adonis	3	16,0	—	—	2	9,0	— 7,0	—	—	0,6
Papaver	4	9,8	—	—	3	21,0	+ 11,2	—	—	2,1
Erysimum	3	11,3	3	17,3	7	20,4	+ 9,1	+ 3,1	+ 6,0	1,8
Sisymbrium	6	12,0	2	7,0	1	14,0	+ 2,0	+ 7,0	— 5,0	1,2
Cardamine	1	8,0	4	13,0	7	11,4	+ 3,4	— 1,6	+ 5,0	1,4
Lepidium	4	12,0	2	12,0	3	21,3	+ 9,3	+ 9,3	± 0,0	1,8
Thlaspi	1	7,0	—	—	3	9,3	+ 2,3	—	—	1,3
Alyssum	5	9,6	8	8,0	13	9,2	— 0,4	+ 1,2	— 1,6	0,96
Linum	3	10,7	—	—	18	13,3	+ 2,6	—	—	1,2
Viola; Subsection *Tricolores*	4	14,8	3	11,3	5	18,6	+ 3,8	+ 7,3	— 3,5	1,3
Mercurialis	1	8,0	—	—	2	28,0	+ 20,0	—	—	3,5
Urtica	3	12,0	—	—	1	24,0	+ 12,0	—	—	2,0
Polygonum	13	14,3	—	—	10	31,8	+ 17,5	—	—	2,2
Rumex	—	—	3	18,3	17	30,8	—	+ 12,5	—	—
Silene	8	12,0	—	—	11	15,5	+ 3,5	—	—	1,3
Stellaria	3	16,5	—	—	8	18,9	+ 2,4	—	—	1,1
Chenopodium	4	9,0	—	—	1	18,0	+ 9,0	—	—	2,0

TABLE 6 (continued).

Genus	Annual species		Biennial or subperennial species		Perennial species		Differences			M_p/M_a
	n	M	n	M	n	M	M_p-M_a	M_p-M_b	M_b-M_a	
Beta	—	—	1	9,0	1	27,0	—	+ 18,0	—	—
Vicia	15	6,6	—	—	7	8,6	+ 2,0	—	—	1,3
Medicago	12	9,1	2	12,0	3	16,0	+ 6,9	+ 4,0	+ 2,9	1,8
Trifolium	9	8,1	2	7,5	10	22,4	+ 14,3	+ 14,9	— 0,6	2,8
Anthriscus	2	9,0	—	—	1	8,0	— 1,0	—	—	0,9
Carum	—	—	1	10,5	1	11,0	—	+ 0,5	—	—
Bupleurum	2	8,0	—	—	1	8,0	± 0,0	—	—	1,0
Alopecurus	3	7,0	1	14,0	2	32,0	+ 25,0	+ 18,0	+ 7,0	4,6
Phleum	1	14,0	—	—	6	11,1	— 2,9	—	—	0,8
Phalaris	2	10,0	—	—	1	10,5	+ 0,5	—	—	1,1
Anthoxanthum	1	5,0	—	—	1	10,0	+ 5,0	—	—	2,0
Hordeum	5	9,1	—	—	4	13,1	+ 4,0	—	—	1,4
Lolium	3	7,0	—	—	1	7,0	± 0,0	—	—	1,0
Festuca	3	9,3	—	—	11	16,2	+ 6,9	—	—	1,7
Bromus	11	10,2	2	28,0	10	20,7	+ 10,5	— 7,3	+ 17,8	2,0
Poa	1	14,0	—	—	11	20,5	+ 6,5	—	—	1,5
Avena	3	16,3	—	—	4	16,5	+ 0,2	—	—	1,0

The correlation between high chromosome number and perennial habit of life is further illustrated by Table 7 (p. 353) and Diagram 1 (p. 354). In Table 7 the chromosome numbers of all species in each of the three categories have been added to three series, which represent all the annual, biennial (or subperennial) and perennial species available. For each series the absolute numbers as well as the percentage values are given. The curves in Diagram 1 have been constructed after the percentage values of the annual and perennial species. — The average values in Table 7 are in the first line of interest. *The average chromosome number of all annual species was found to be 10,65, the corresponding figures of the biennial and perennial species being 15,50 and 16,95. Thus the value of the perennial species is not less than 59 per cent higher than that of the annual species.* The marked skewness of the curves prevents calculation of the standard errors, but from the distribution in the different series it can scarcely be doubted that the annual series is significantly different from the perennial series. The biennial and subperennial species seem to be intermediate.

With regard to the annual and perennial series it is striking that

TABLE 7. *Chromosome numbers in annual, biennial and perennial species of 48 genera.*

	Gametic chromosome numbers																							n	M
	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105			
Annual species	22		103	43	20	18	1	—	2															209	10,65
	10,5		49,3	20,6	9,6	8,6	0,5	—	1,0															per cent	
Biennial (or subperennial) species	1		13	10	11	7	3	1	1															47	15,50
	2,1		27,7	21,3	23,4	14,9	6,4	2,1	2,1															per cent	
Perennial species	27		100	58	41	51	9	18	4	3	1	7	—	1	2	—	—	—	—	2	—	2		326	16,95
	8,3		30,7	17,8	12,6	15,6	2,8	5,5	1,2	0,9	0,3	2,1	—	0,3	0,6	—	—	—	—	0,6	—	0,6		per cent	

all species with the haploid numbers ranging from 40 to 105 are perennial. Above a certain chromosome level it does not seem to be possible for a plant species to complete its full development in one year. — Another feature which should be emphasized is the fact that the maximum class is the same in the annual and perennial series, being

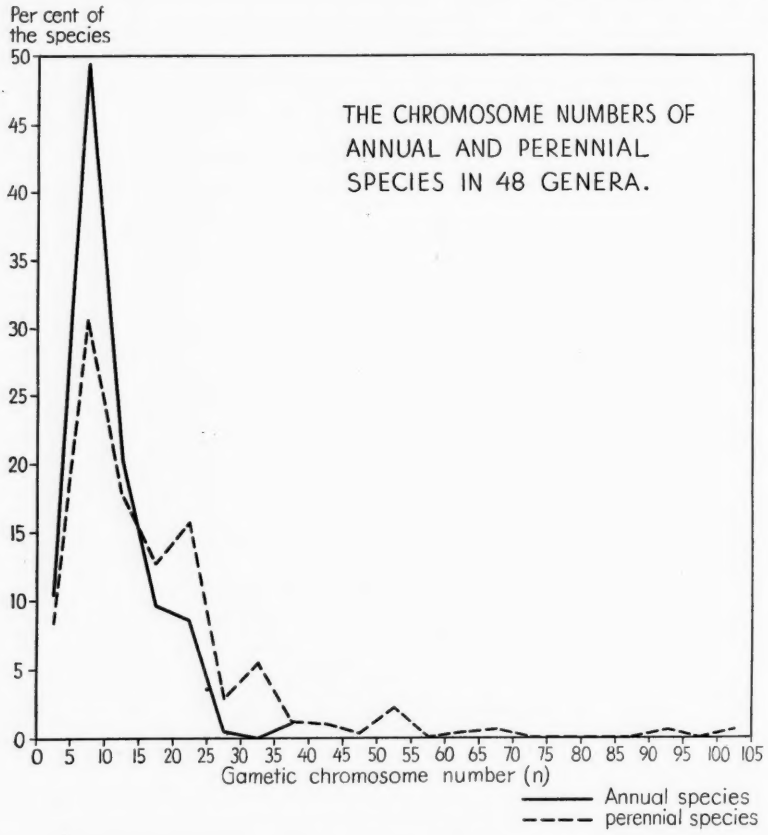
Per cent of the species
THE CHROMOSOME NUMBERS OF ANNUAL AND PERENNIAL SPECIES IN 48 GENERA.
0 5 10 15 20 25 30 35 40 45 50
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100 105
Gametic chromosome number (n)
Annual species
perennial species

Diagram 1. The chromosome numbers of annual and perennial species in 48 genera.

represented by species with 5—10 chromosomes (haploid number). However, not less than 49,3 per cent of the annual species belong to this class as compared with 30,7 per cent of the perennials.

The fact that the maximum class is the same in annuals and perennials may be understood by a renewed scrutiny of Table 6. It is evident

from this table that the different genera behave very differently with respect to the average correlation found. In some exceptional genera, *e. g. Linaria* and *Alyssum*, the difference between annual and perennial species has nothing to do with polyploidy but must be ascribed to specific genes. The presence of a number of such genera in the material studied will evidently tend to produce a joint maximum class for annuals and perennials. That the difference between annual and perennial habit of life may be caused by specific genes is evidently true also of the genus *Crepis*, at least the subgenus *Barkhausia*. In the subgenus *Eucrepis*, however, there may be some influence of polyploidy upon the average value of the perennials (7,1), which is somewhat higher than the average value of the annuals (4,9). Unfortunately, I have not obtained information as to the life forms of a number of American species in this subgenus, having rather high chromosome numbers. Even if these are perennial, which is probable, the result may not necessarily come into conflict with the conclusion of BABCOCK and CAMERON (1934) that in *Crepis* the perennial species are older and more primitive than the annual ones. This may hold good of most of the *Crepis* species. In the light of the present results, however, it seems probable that some *Crepis* species are secondary perennials, which have arisen from annual species with lower chromosome numbers.

In several genera the correlation between chromosome number and type of life form is very striking. A good example is *Senecio*, in which 7 annual species had the average value of 13,6, the corresponding values of 2 biennials and 11 perennials being 17,0 and 28,5. Another good case is *Polygonum*. In this genus 13 annual species had the average value of 14,3, 10 perennial species having the corresponding figure of 31,8. — Concerning several other genera, I must refer the reader to a detailed study of Table 6.

The most common case, however, is probably that the perennial species of the genus owe their perennial habit either to specific genes or to polyploidy. In such genera the general correlation may be observed but less strikingly than in such genera as *Senecio* and *Polygonum*, in which the connection between polyploidy and long duration of life must be very close. The genera showing such typical correlation, however, cannot be sharply distinguished from the other genera.

From all the data presented above it is quite evident and indisputable that there is a close connection between chromosome number and type of life form. This connection must ultimately be due to a correlation between chromosome number and rate of cell division.

This was found to be typical of experimental autopolyploids, which are also characterized by a retardation in the rate of development. The causal connection between the two phenomena, the retarded development of experimental autopolyploids and the high chromosome numbers of wild perennial species, is especially clear from the fact, mentioned earlier in this paper, that the autotetraploid maize strain, produced by RANDOLPH, was found to be perennial in contrast to diploid annual maize. — Although it may seem paradoxical we have thus the right to conclude that the perennial life form of many plant species is quite comparable to the retarded development of the tetraploid pupae and larvae of the moth *Solenobia* or the prolonged vegetation period of tetraploid tomato.

Since these connections may now be regarded as in the main solved another more important conclusion may be drawn. *A large number of perennial species must have originated from annual types with lower chromosome numbers.* If this conclusion were not correct the correlation between chromosome number and type of life form would be impossible to understand. — Considering the behaviour of experimental autopolyploids, we may further conclude that *the evolution of these species has essentially been caused by quantitative chromosome alterations.* Whether this chromosome increase implies strict autopolyploidy or allopolyploidy is a question of minor importance. We have reason to believe, however, that *the effect observed is chiefly due to the reduplication of entire genomes.*

VI. AUTOPOLYPLOIDY AS THE CAUSE OF ANEUPLOIDY AND POLYMORPHISM.

In the preceding chapters the importance of autopolyploidy for the production of polyploid chromosome races and species has been discussed. However, autopolyploidy may also have important secondary consequences. A considerable amount of evidence demonstrates that occasional or permanent aneuploidy may occur among derivatives from autopolyploids.

Considering first the occasional aneuploidy, it was mentioned above (pp. 314—316) that in several polyploid chromosome races, just as in experimental autopolyploids, a certain percentage of aberrants appear in each generation. This has been observed, *e. g.* in *Biscutella laevigata*, *Silene ciliata*, *Pentstemon azureus* and *Dactylis glomerata*, and shows that gametes and zygotes with slightly deviating chromosome numbers are

viable. — The chances that such gametes and zygotes will be viable are evidently greater in an autopolyploid than in an allopolyploid. The presence or absence of an extra chromosome in an autotetraploid *AAAA* will cause a less severe disturbance than in an allotetraploid *AABB*. Further, as demonstrated by the *Datura* work, the effect of the presence or absence of extra chromosomes is inversely proportional to the degree of polyploidy. — In *Dactylis* I have observed that triploid individuals have very poor pollen and are completely male sterile, as the anthers do not dehisce. In pentaploids, on the other hand, fertility is excellent and more than 90 per cent of the pollen may be good. In triploids, as well as in pentaploids, pollen grains with widely different and chiefly aneuploid numbers are formed, but in the pentaploids, in contrast to the triploids, the genes necessary for viability are reduplicated so many times that aneuploids has no severe consequences. A similar situation is met with when the fertility and vigour of $2n + 1$ and $4n + 1$ types are compared.

Besides the cases of intraspecific chromosome races mentioned, several other polyploid species are known to have an oscillating chromosome number (cf. the list given by DARLINGTON, 1932, p. 203). In most cases of this kind there can be no hesitation as to which number should be regarded as the typical one (as *e. g.* in *Crepis biennis*, cf. BABCOCK and SWEZY, 1935) but in other cases it may be impossible to distinguish between aberrants and normal individuals. The transitions seem to be continuous from quite stable species and races to those in which there is no typical chromosome number.

The evidence available indicates that such species with oscillating chromosome numbers are generally autopolyploid. A very striking example of this kind is *Prunus laurocerasus* (MEURMAN, 1929 b). The chromosome number in this species is very high ($2n = 170—180$) and there is no haploid chromosome number in the strict sense, meiosis being irregular and resulting in gametes with various chromosome numbers. The autopolyploid nature of the species is strongly indicated by the frequent occurrence of multivalent associations at meiosis. The author (l. c. p. 93) stresses the importance of autopolyploidy for the origin of aneuploid series and points to the genera *Viola* and *Carex* as probable examples of this kind.

In several *Saxifraga* species the chromosome number is also unstable (SKOVSTED, 1934). In *S. granulata*, *e. g.*, the somatic number was found to vary between 46 and 60 without any noticeable morphological effect. For this reason SKOVSTED concludes that the vital genes must

be repeated so many times that one chromosome more or less does not effect the physiological balance. The frequent occurrence of multivalent associations is supposed to be due to structural changes but may probably in part be the expression of an autopolyploid condition. At all events it seems probable that the material studied is of autopolyploid origin, though structural changes may have arisen secondarily.

A similar case is met with in *Poa alpina* (MÜNTZING, 1932 b and unpublished results). In sexual strains of this species the somatic chromosome number may have any value between 21 and 33 (apart from single individuals with higher numbers, which arise through the function of unreduced gametes). It has not yet been possible to find any sure correlation between chromosome number, vigour and fertility in this material and there is no typical haploid number. Meiosis is irregular and characterized by the presence of multivalents in addition to bivalents and univalents. The basic number of related species is seven.

A fourth instance of the same thing and one of the first cases described of a species with oscillating chromosome number is represented by *Viola canina* (CLAUSEN, 1931 a). Danish material of this species was found to have $2n = 40 +$ a varying number of extra chromosomes or fragments. This variation has no noticeable morphological effect, which indicates that the extra chromosomes are duplicates of other chromosomes. This possibility is supported by the occasional occurrence of quadrivalents. — Though the evidence available does not permit the conclusion that *Viola canina* is an autopolyploid species, there are many other indications that chromosome duplication has played an important rôle for species formation and polymorphism in this genus in general. The following data may be quoted.

As in *Viola canina*, certain segregation products from the cross *V. tricolor* × *arvensis* have constant morphology in combination with varying chromosome number (CLAUSEN, 1926, p. 101). This is thought to be due to duplicate chromosomes. The occurrence of duplicate genes for some characters has indeed been demonstrated by genetical data. In a cross between two *tricolor* strains the basal gene for colouring was found to segregate according to the ratio 63 : 1 (CLAUSEN, 1926, p. 31). In a later paper (CLAUSEN, 1931 b, p. 294) the author states that there appears to be a close coincidence between the degree of polymery and the degree of polyploidy within the *Melanium* section, monohybrid, dihybrid and trihybrid ratios for the same characters being obtained in different species. — This reduplication of chromosomes may also be responsible for the high fertility in F_1 of the species cross *V. tricolor* ×

arvensis (cf. CLAUSEN, 1926). The parent species are approximately tetraploid (*tricolor*, n = 13) and hexaploid (*arvensis*, n = 17) as the original basic number of the genus is supposed to be 6 (CLAUSEN, 1929). If the genomes are rather similar it is comprehensible that the F_1-hybrid, which is approximately pentaploid, will have quite good fertility in spite of considerable meiotic irregularities. Just as in the pentaploid *Dactylis* types discussed above (p. 357) most gametes will be viable owing to the reduplication of all necessary chromosomes.

In *Viola* there are polyploid series with different basic numbers but several deviations from these series occur. *V. tricolor* and *arvensis* represent constant aneuploid types, the former probably being a 4n + 2 type, the latter corresponding to the formula 6n — 2 (cf. CLAUSEN, 1927, 1929). New aneuploid types, which are constant, have also been experimentally produced. For example, a new *arvensis* type with 2n = 32 instead of 34 was obtained in the progeny of a cross between two *arvensis* strains. This is taken as evidence that species with aneuploid numbers, and among them *tricolor* and *arvensis* themselves, may have arisen in a similar way (CLAUSEN, 1926, p. 54). It is highly probable that a more or less pronounced degree of autopolyploidy is a necessary condition for the production of such successful and constant aneuploid derivatives, which have also been obtained in the progeny of *tricolor* × *arvensis* hybrids. — Parenthetically I may mention that from the material of *Poa alpina*, studied by the present writer and referred to above, it was possible to select a new true-breeding or almost true-breeding strain with 2n = 22. This seems to indicate the formation of a new basic number 11 from the original basic number of 7.

Returning to *Viola*, the strongest evidence of autopolyploidy in this genus remains to be considered. Firstly, some species, included in Table 1 of the present paper and discussed above, are known to be autopolyploid or most probably autopolyploid. This is true of *Viola elatior* and *V. crassa* (Cases 45—46, Table 1). There are indications that other species are quite analogous to these cases. — Secondly, the occurrence of autosyndesis has been reported for several species hybrids in this genus, *e. g. lutea* × *elegantula*, *tricolor* × *Battandieri*, *tricolor* × *nana* and it possibly occurs also in *tricolor* × *arvensis*, F_1 (CLAUSEN, 1926, 1931 b). — Multivalents seem to be rare in the polyploid *Viola* species but this may be due to a low chiasma frequency or to secondary structural changes. That structural changes have been involved in species differentiation in *Viola* is evident from the presence of multiple associations in certain F_1-hybrids, though the parent species have only

bivalents (CLAUSEN, 1931 b). Nevertheless, these structural changes have only in part obliterated the numerous indications of autopolyploidy.

Summarizing the conditions in *Viola* on the basis of the genetical and cytological results of CLAUSEN and MIYAJI, we may conclude that in this genus typical autopolyploidy or reduplication of single chromosomes has been largely involved in species formation. This has made possible the origination of aneuploid chromosome numbers, slightly deviating from the multiple series. The reduplication of chromosomes is responsible for the high fertility of certain polyploid F_1-hybrids and for the viability of segregation products with deviating chromosome numbers. In short, *Viola* seems to be an excellent example of the fact that aneuploidy and polymorphism may be the secondary consequences of autopolyploidy.

There is reason to believe that as regards the variation in chromosome number several other genera in the main belong to the same type as *Viola*. Of these only *Crepis*, *Carex* and *Iris* may be briefly considered. In *Crepis* the following haploid chromosome numbers are most common: 3, 4, 5, 6, 7 and 8. These numbers seem to indicate that complete aneuploidy is characteristic of the genus and that polyploidy has played little or no part in the evolution of *Crepis* (cf. DARLINGTON, 1932, pp. 215—216). This is not the case, however, as demonstrated by BABCOCK and his co-workers (cf. BABCOCK and CAMERON, 1934). Amphidiploidy and autopolyploidy are among the most important evolutionary processes in the genus, though this is not evident from a comparison of the chromosome numbers alone.

The situation in *Iris* is even more striking. According to SIMONET (1934 c), 22 different haploid chromosome numbers are known in this genus and among them every number between 8 and 24 is represented. This apparent aneuploidy, however, also includes 8 different polyploid series (l. c. pp. 324—325), and from several facts, previously discussed in the present paper, we know that autopolyploidy must have been a most important factor in the evolution of the *Iris* species. Under such circumstances it is conceivable that viable aneuploid types may arise, *e. g.* in the progeny of unbalanced autopolyploids (triploids, pentaploids) or by hybridization between different species or varieties. If these species are both autopolyploid and have different basic numbers new constant species with a new basic number may arise. This has been experimentally realised in the case of *I. autosyndetica*, discussed above (p. 338). This synthetic species has $n = 23$ and arose from a

cross between parent species with n = 22 and n = 24 respectively. The origin of aneuploidy in *Iris*, as in other genera, may of course in part be caused by purely structural changes, but as in *Viola* and *Crepis* aneuploidy and polymorphism may largely be the secondary consequences of autopolyploidy.

In the light of recent results in *Crepis* and *Iris* it seems probable that the classical aneuploidy in the genus *Carex* (HEILBORN, 1924) is also of a secondary nature and that polyploidy even in this genus, as well as in *Scirpus*, may have been of prime importance for species formation (cf. MEURMAN, 1929 b; MÜNTZING, 1933 b). This view gains support from the finding of HEILBORN (1932) that *Carex glauca* is probably an autotetraploid (cf. above p. 335). Further, BRUUN (1932, pp. 146 and 211—213) has pointed out that in comparison with the number of sections in this genus the number of species hitherto examined in *Carex* is rather small. As the sections may have different basic numbers (as in *Iris*, *Primula* and many other genera) the striking aneuploidy in *Carex* may only be apparent. It is possible that the gametic and zygotic selection, which in most Angiosperm genera tends to preserve the polyploid series (cf. MÜNTZING, 1933), is weaker than usual in *Carex*. As in *Viola* and *Iris* this may be due to complete or partial autopolyploidy. On the other hand, deviations from the multiple series is no sure criterion of autopolyploidy. As discussed above, *Chrysanthemum* and *Galium* are two genera in which autopolyploidy has played a most important rôle, but nevertheless these genera represent excellent instances of strict polyploidy.

It would lead too far to give a complete survey of the relations between autopolyploidy, aneupolyploidy and polymorphism. The instances given, however, should suffice to show that these phenomena are intimately related and that autopolyploidy may have important secondary effects.

VII. CONCLUDING REMARKS. THE SIMILARITY BETWEEN AUTO- AND ALLOPOLYPLOIDY.

In a preceding chapter (p. 310) the difference between auto- and allopolyploidy was discussed. Even from a terminological point of view it was found to be difficult to find a border-line between these two categories, and this difficulty may be even greater in concrete cases. DARLINGTON (1932, p. 170) points out that allopolyploids show a gradation in behaviour from those with slight to those with strong differentia-

tion between the homologues, derived from opposite parents. At the extreme in one direction is such a hybrid as *Crepis rubra* × *C. foetida* (POOLE, 1931), in which the difference between the parents is so slight that the diploid has complete pairing and the tetraploid derived from it behaves like an autopolyploid. In an intermediate position is, *e. g.*, *Primula Kewensis* and at the extreme in the other direction *Raphanus-Brassica.*

Other border-line cases between auto- and allopolyploidy are represented by the tetraploid derivatives obtained from the cross *Fragaria bracteata* × *Helleri* (cf. LILIENFELD, 1933) and from the cross *Aquilegia chrysantha* × *flabellata* (SKALINSKA, 1933 a and b). A natural species of much the same kind is represented by *Sorghum halepense*, studied by HUSKINS and SMITH (1932, 1934). Chiefly on account of chromosome morphological data, these authors conclude that the species in question must be allopolyploid. However, *Sorghum halepense* seems to have many features in common with autopolyploids. — At meiosis 20—28 of the forty chromosomes are present as bivalents, the rest as quadrivalents or higher associations. As LONGLEY (1932) has found a *Sorghum* species with $n = 5$, *S. halepense*, should be regarded as an octoploid. This may explain the occurrence of associations of more than four chromosomes in this species as well as the occasional formation of multivalents in species with $2n = 20$, having half the number of *halepense*. Consequently, the occurrence of multivalents in *halepense* indicates an autopolyploid condition. This is further supported by other facts. *S. halepense* is the only perennial *Sorghum* species and the correlation between high chromosome number and perennial habit of life may be regarded as indirect evidence of autopolyploidy (cf. Ch. V, p. 340). Further, LONGLEY (1932) reports that *S. halepense* is hardly distinguishable morphologically from the annual species *S. sudanensis*, which has half the chromosome number of *halepense*. This close morphological similarity between the 8n and 4n species strongly indicates an autopolyploid relationship. The observation that *halepense* has another geographical distribution than most annual wild forms (cf. HUSKINS and SMITH, 1932, p. 241) also accords very well with the fact that autopolyploid chromosome races have generally another distribution than their diploid relatives. Finally, it should be mentioned that *halepense* is very much incompatible with the annual forms (cf. HUSKINS and SMITH, 1932, pp. 241—242). Such incompatibility, however, is characteristic not only of experimental and natural autopolyploids but is generally found also between allopolyploids and their

original parents (cf. above p. 327). — Considering all data, it seems probable that the constitution of *Sorghum halepense* is rather similar to that of *Crepis biennis*. In both species there seem to be slight structural differences between some of the genomes, but it is uncertain whether these are of primary or secondary origin. At any rate, the genomes are largely homologous and this homology is probably much greater and much more important than the differences present.

The same statement may be true of allopolyploids in general. Even in extreme cases, when the parent species belong to different genera, as *e. g. Raphanus-Brassica* and *Triticum-Secale*, the number of genes they have in common must be much greater than the number of different genes. The differences between related species and genera are most probably rather superficial as compared to the genes which control that the species are plants belonging to a certain class, order and family. — All these genes, which the species crossed have in common, are doubled in the allopolyploids just as well as the genes, causing the parent species to be different. Hence, *allopolyploid species are always partially autopolyploid and the different genomes in an allopolyploid are probably never completely different. Only autopolyploidy, not allopolyploidy, may be absolute.*

As an expression of this similarity allopolyploids have in fact many properties in common with autopolyploids. Without going into details it may be stated that allopolyploids have generally larger cells than the parent species and probably as a consequence of this greater cell size they generally present a number of gigas characters. These characters may consist in a more robust habitus, greater height, thicker stem and larger leaves; further, the flowers, fruits and seeds may be larger (cf. MÜNTZING, 1931 b). In short, allopolyploids, though in the main morphologically intermediate between the parents crossed, may present just the same gigas characters as were found to be characteristic of autopolyploids. On an average, however, the gigas characters are less marked in experimental allopolyploids than in autopolyploids. Further, in those cases in which the F_1-hybrid shows hybrid vigour the gigas characters of the allopolyploid product may partly be due to homozygosity of the genes causing vigour in F_1. Nevertheless, as cell size in allopolyploids, in the same manner as in autopolyploids, is correlated with chromosome number, the gigas characters are probably in the first line caused by the greater cell size and not by genes having a complementary effect. — In some cases the allopolyploids are inferior in viability compared to the parent species. As in the autopolyploids this

may be due to specific properties of the species involved or to the fact that the chromosome optimum has been exceeded.

Whether allopolyploids have new physiological properties which go beyond those of the parent species has not been subject to much attention but is indicated by the results of KOSTOFF and AXAMITNAJA (1935 a) cited above (p. 297). If *Sorghum halepense* is to be regarded as an allopolyploid it should be remembered that this species has a specific geographical distribution and is perennial in contrast to the other *Sorghum* species. As argued above these new properties are probably correlated with the quantitative increase in chromosome number. — The same may be true of the allopolyploid *Spartina Townsendii*, which has rather recently arisen from crosses between *S. alterniflora* and *stricta* (HUSKINS, 1931). *S. Townsendii* is an extremely successful new species, having spread widely from its point of origin, and has almost completely eliminated its parent species wherever it has come into competition with them. *S. Townsendii* is evidently not merely intermediate between the parent species but correlated with the increased chromosome number it has obtained new important physiological properties.

The similarity between auto- and allopolyploidy is also evident by the fact that certain allopolyploids are known to have polymeric factors, the number of which corresponds to the number of genomes present. Trimeric ratios are well-known in the hexaploid species *Triticum vulgare* and also occur in *Avena sativa* (ÅKERMAN, 1922 and recent unpublished results; ÅKERMAN and MÜHLOW, 1933). In the tetraploid *Galeopsis Tetrahit* I have observed (MÜNTZING, 1930 a) the segregation ratio 15 : 1 with regard to flower colour as well as stem colour. As already mentioned (p. 358) a similar case is met with in *Viola*.

With regard to fertility there is on an average a characteristic difference between auto- and allopolyploids, the latter being more fertile. This is no doubt correlated with a more regular and sometimes quite regular meiosis in the allopolyploids, but as discussed above (pp. 316—322) regular meiosis is no reliable criterion of complete fertility. Physiological influences caused by the constitution of the mother plant may bring about a reduction in fertility, which is often considerable. It is probable that similar influences may act upon fertility also in allopolyploids and, indeed, a number of allopolyploids are known (cf. DARLINGTON, 1932, pp. 173—174; SANSOME and PHILP, 1932, p. 329; SHARP, 1934, p. 367) in which fertility is too poor to be caused by

meiotic irregularities alone. Consequently, also with respect to fertility auto- and allopolyploids have some common features.

In the introduction to the present paper the differences in opinion as to the evolutionary value of autopolyploidy were discussed. The data gathered above strongly emphasize the importance of autopolyploidy or better the importance of quantitative chromosome alterations, whether these are absolute or partial. In the preceding chapters it was demonstrated that such alterations may have marked morphological effects and may lead to new physiological properties. It has also been shown that they are responsible for the origin of barriers of incompatibility and sterility. These barriers cause discontinuity and are a necessary condition for the formation and preservation of polyploid series (MÜNTZING, 1933 b). This discontinuity may further facilitate additional differentiation by means of gene mutations and structural changes. *Thus it is evident that quantitative chromosome alterations have played a very important rôle in the evolution of the higher plants.*

SUMMARY.

1) As opinions concerning the evolutionary importance of autopolyploidy are very divergent the present writer has made an attempt to elucidate this problem by some new contributions. The data gathered have chiefly been obtained from an analysis of intraspecific polyploidy and experimental autopolyploidy. Additional evidence has been derived from a comparison between intra- and interspecific polyploidy, from cases of autosyndesis and from a study of the correlation between chromosome number and type of life form.

2) Intraspecific chromosome races are characterized by quantitative morphological differences and positive correlation between chromosome number and gigas characters. The morphology of polyploid chromosome races is essentially similar to that of experimental autotetraploids.

3) The chromosome races are generally ecologically different. This is comprehensible inasmuch as experimental autopolyploids present a series of new physiological characters.

4) Intraspecific chromosome races are generally separated from each other by barriers of incompatibility and sterility. In this respect they are quite similar to experimental autopolyploids.

5) In most polyploid intraspecific chromosome races chromosome association at meiosis is of the same type as in experimental autopoly-

ploids. In combination with the other data this demonstrates that most polyploid intraspecific chromosome races are autopolyploid.

6) As far as constancy is concerned, polyploid chromosome races and experimental autopolyploids behave in the same way. As regards fertility, however, they are different, but this difference seems explicable by the fact that the chromosome races, in contrast to the experimental autopolyploids, have been subject to natural selection.

7) With regard to morphology, ecology and chromosome association (in the p.m.c.) intraspecific chromosome races in a number of apomictic species have the same essential properties as were found in chromosome races of sexual species.

8) The formation of autopolyploid chromosome races is an important factor in the evolution of new species. This is evident from a morphological and ecological comparison between intra- and interspecific polyploidy and from an analysis of the causes of incompatibility. The barriers of incompatibility between species with different chromosome numbers are mainly due to purely quantitative conditions. The occurrence of a number of species in which the mode of meiosis reveals their autopolyploid constitution confirms the conclusion that new species may be formed by intraspecific autopolyploidy.

9) The numerous cases of autosyndesis in hybrids emphasize the evolutionary significance of quantitative chromosome increase.

10) In 48 genera, comprising 582 species, correlation between chromosome number and type of life form was observed. The perennial species in a genus have in most cases a higher average chromosome number than the annual species of the same genus. In the material studied the average chromosome number of the perennial species was found to be 59 per cent higher than that of the annual species. The biennial and subperennial species seem to be intermediate.

11) Autopolyploidy may have secondary effects, of which aneuploidy and the formation of new basic numbers are the most important.

12) The similarities between allo- and autopolyploids are more important than the differences and are due to the fact that all allopolyploids are partially autopolyploid. Purely quantitative chromosome alterations, whether absolute or partial, have played a very important rôle in the evolution of the higher plants.

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Svalöf, Cyto-Genetic Department of the Swedish Seed Association, December 1935.

APPENDIX.

After this manuscript had been completed I received two papers by HOMEYER (1935) and FAGERLIND (1936), which support the conclusions drawn in the present paper. HOMEYER finds that among the *Galium* species studied by him the polyploid types are more hardy and northern than diploid types. »Es wurde festgestellt, dass mit der Eroberung neuen Lebensraumes, ausgehend vom wärmeren Klima, bei den Galien in den meisten Fällen ein Polyploidwerden einhergeht.» — FAGERLIND, also working with *Galium*, has observed that cases of seasonal dimorphism may be correlated with differences in chromosome number. A summer type of *G. verum* (f. *praecox*) is diploid, the autumn type tetraploid. In the same way the summer type of *G. palustre* is diploid, the autumn type, f. *elongatum*, octoploid. FAGERLIND considers that the more robust autumn types are autopolyploids derived from the diploid *aestivalis* forms and suggests that similar correlations may be found in other genera with seasonal dimorphism. These results are in excellent accordance with the correlation between high chromosome number, slow rate of development and perennial habit of growth, discussed in Ch. V of the present paper.

The chapter dealing with the physiological consequences of chromosome doubling (pp. 293—298) may also be supplemented thanks to a recent paper by G. F. GÖTHLIN [»Biologiska bestämningar av halten av antiskörbjuggsvitamin (vitamin C; askorbinsyra) hos 12 av de viktigaste i Sverige odlade äpplesorterna». — Kungl. Landtbruks-Akademiens Handlingar och Tidskrift, Nr. 7, 1935, pp. 884—944. With a summary in English]. — It was mentioned above (p. 296) that according to SANSOME and ZILVA (1933) the vitamin C content of tomatoes is about twice as high in tetraploids as in diploids. This result strengthened the evidence obtained by CRANE and ZILVA (1931) that also in the case of apples there is a connection between the vitamin C content and the number of chromosomes. — Now, this connection may be further studied thanks to the work of GÖTHLIN, who has studied the vitamin C content in a number of apple varieties. By means of a prophylactic method of feeding guinea-pigs, in which a normal microscopic structure in the lamellae of the guinea-pigs molar teeth was taken as a criterion of complete protection against

scurvy, GÖTHLIN (l. c.) determined the lowest »micro» preventive dose against scurvy in guinea-pigs of twelve kinds of apples grown in Sweden. On the basis of additional experiments GÖTHLIN could determine the quantity of ascorbic acid (vitamin C) per 100 gr. of the apple. This quantity was found to range from 2,0 to 22 mg. GÖTHLIN cites the results of CRANE and ZILVA (1931) but does not report the chromosome numbers of the varieties he has tested himself. — The present writer utilized the lists of chromosome numbers in apple varieties recently published by HEILBORN (1935) and found that of the 12 varieties studied by GÖTHLIN 8 were diploid, 4 triploid. The average contents of ascorbic acid in these 8 diploid varieties is *5,38* mg., the corresponding value of the four triploid varieties being *12,00* mg. — In addition to these 12 varieties GÖTHLIN has tested a number of other varieties by simplified and less reliable methods and also reports the probable contents of ascorbic acid in a number of foreign apple varieties. — I have also looked up the chromosome numbers of most of these additional varieties and found the same correlation. Adding all the data available the average contents of ascorbic acid was found to be *12,66* ($\pm$ *2,50*) in six triploid varieties and *5,58* $\pm$ *0,94* in seventeen diploid varieties. After these results the occurrence of a correlation between chromosome number and vitamin C contents in the apples can scarcely be doubted. This emphasizes once more that quantitative chromosome changes may have important physiological consequences.

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CONTENTS.

I. Introduction 263
II. Intraspecific chromosome races 266
1. The morphology of intraspecific chromosome races 269
2. Comparison between the morphology of experimental autotetraploids and polyploid chromosome races 281
3. The ecology of intraspecific chromosome races 288
4. The physiological consequences of chromosome doubling 293
5. Comparison between the physiological properties of chromosome races and experimental autopolyploids 299
6. The result of crosses between intraspecific chromosome races 300
7. Are the intraspecific chromosome races auto- or allopolyploid? 304
8. Fertility and constancy in intraspecific chromosome races and experimental autopolyploids 313
9. Intraspecific chromosome races in apomictic species 322
III. The relation between intra- and interspecific polyploidy 324
1. Morphology and ecology 325
2. Incompatibility 326
3. Meiosis 334
IV. Evidence from autosyndesis 336
V. Comparison between the chromosome numbers of annual and perennial species 340
VI. Autopolyploidy as the cause of aneuploidy and polymorphism 356
VII. Concluding remarks. The similarity between auto- and allopolyploidy 361
Summary 365
Appendix 367
Literature cited 368

ÜBER EINE IN DER NATUR GEFUNDENE GIGASFORM VON POPULUS TREMULA

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ALS der Verfasser zusammen mit dem Grafen PH. BONDE, Bosjökloster am 3. Juni 1935 die Bedingungen eines im Grossen angelegten Obstbaues auf der Halbinsel Lillö, Ringsjön näher studierte, fiel ein Bestand der Espe (*Populus tremula* L.) auf, der sich in der ganzen Laubkrone durch erheblich grössere, dunklere Blätter als bei der in unmittelbarer Nähe wachsenden gewöhnlichen Espe kennzeichnete (vgl. Fig. 1 und 2). Der Unterschied an Blattgrösse war so auffallend gross, dass an einer erheblichen Diskontinuität der Blattgrösse im Vergleich mit der verhältnismässig kleinen Schwankung der Blattgrösse bei verschiedenen auf Lillö wachsenden Beständen der gewöhnlichen Espe nicht zu zweifeln war.

Da bei näherer Untersuchung die Vergrösserung nicht nur die Laubblätter, sondern auch Blattstiele, Knospen, Zweige, Staubfäden usw. betraf, m.a.W. da der abweichende Typus mit früher bekannten Gigastypen anderer Arten grosse allgemeine Ähnlichkeit zeigte, musste sofort an eine multiple Erhöhung der Chromosomenzahl gedacht werden, die auch durch die hier anschliessende Untersuchung MÜNTZINGS (1936) bestätigt wurde, indem die gewöhnliche *Populus tremula* diploid ist mit $2 \times 19 = 38$ Chromosomen in der Zellkerne, wogegen die hier beschriebene *Populus tremula gigas* triploid ist und demnach $3 \times 19 = 57$ Chromosomen oder eine nahe daran sich anschliessende Chromosomenzahl besitzt.

Der Bestand von *Populus tremula gigas* in Lillö umfasst mehrere Hundert erwachsener Bäume, die durch vegetative Verzweigung einer ursprünglichen Mutterpflanze erwachsen sind. Sie stellen m.a.W. eine einzige Klone typischer Art dar, mit vollständiger Ähnlichkeit aller Bäume untereinander. Die Klone ist männlich.

Die Gigasespe wächst viel schneller als die gewöhnliche Espe, hat durchschnittlich erheblich breitere Jahresringe und demgemäss eine bedeutend grössere jährliche Holzproduktion. Sehr auffallend ist ferner ihre bedeutend grössere Resistenz gegen Angriffe von *Polyporus*. Die Bäume der Gigasespe haben ferner einen geraderen, schöneren Wuchs

Fig. 1. *Populus tremula gigas.* Laubkronenblatt der Gigasespe von Lillö. — Natürliche Grösse.

als die nebenbei wachsenden gewöhnlichen Espen. Infolge des kräftigeren Wuchses gedeihen die Riesenespen gut in Mischung mit den anderen wilden Laubbäumen in Lillö, d.h. Linden, Ahornen, Ulmen usw., wogegen die schwächeren gewöhnlichen Espen meistens nur an den Rändern der Laubholzbeständen, und daher in geringerer Menge, vorkommen.

Fig. 2. *Populus tremula.* Laubkronenblatt der gewöhnlichen Espe von Lillö, in unmittelbarer Nähe der Gigaespe wachsend. — Natürliche Grösse.

Da ein Vergleich zwischen der Gigaespe und der nebenbei wachsenden gewöhnlichen Espe mit Hinsicht auf ihre anatomischen, physiologischen, holzchemischen, forstlichen und technischen (in Streichholzindustrie, Papierindustrie und Textilindustrie) Eigenschaften in einer Reihe von Spezialarbeiten erfolgen dürfte, werde ich auf die jetzt in diesen Richtungen vorliegenden preliminären Ergebnisse hier nicht eingehen.

Wann und wie die Gigasespe aus der gewöhnlichen Espe entstanden ist, darüber lassen sich vorläufig nur Vermutungen aufstellen. Da die morphologischen Eigenschaften der gewöhnlichen Espe (von den Grössendifferenzen abgesehen) durchaus beibehalten sind, spricht nichts für eine allopolyploide Entstehungsweise, und es ist deshalb unbedingt an eine autopolyploide Entstehung zu denken, was auch durch die Befunde MÜNTZINGS noch weiter bekräftigt wird. Da Temperaturchocke bekanntermeise mehrmals Chromosomenvermehrung ausgelöst haben, hat eine zuerst vom Gutsbesitzer A. BERG VON LINDE, Axelvold, aufgestellte Hypothese, dass Waldbrände eventuell die auslösende Ursache einmal gewesen wären, eine gewisse Wahrscheinlichkeit für sich.

Institut für Vererbungsforschung, Svalöf, Februar 1936.

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THE CHROMOSOMES OF A GIANT POPULUS TREMULA

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LAST summer Professor NILSSON-EHLE called my attention to a giant form of *Populus tremula*, which he had detected at Lillö on the shore of Lake Ringsjön in the middle of the province of Scania, South Sweden. As described by NILSSON-EHLE (1936) in another place in this volume (pp. 379—382), the aspen type in question is very vigorous, the extremely large leaves being especially characteristic. On account of these gigas properties this new type was suspected to have a higher chromosome number than ordinary *Populus tremula*. This suspicion was strengthened by measurements of the size of the stomata. For this purpose leaves of the gigas plants were used in comparison with leaves of ordinary aspen from the same locality. The stomata of the gigas type were found to be larger than those of the normal type, the average values being $10{,}76 \pm 0{,}13$ and $8{,}58 \pm 0{,}14$ respectively. The distribution of the two series is represented in Table 1.

The chromosome number has now been determined by root tip counts as well as by a preliminary study of meiosis. The gigas type proved to be triploid or approximately triploid, having $2n = \pm 57$. Ordinary *Populus tremula*, from Lillö, as well as from two other localities in the same province (Källstorp and Kågeröd), was found to have $2n = 38$, the same number as previously reported for this species by BLACKBURN and HARRISON (1924).

Root tips were obtained by planting root cuttings in pots in the middle of December, and subjecting them to artificial electrical light in a green house. After a few weeks the leaves had developed and at the same time plenty of root tips could be obtained. These were fixed in two fixatives, diluted chrome-acetic-formalin and La Cour 2BE. Only the former fixative gave satisfactory results. Even with this fixative, however, it was rather difficult to determine the somatic chromosome number accurately. On an average the chromosomes are very small, but the idiogram is composed of chromosomes belonging to several different size classes. Under such circumstances it was sometimes very difficult to decide between the possibility of one long chromosome with

a median constriction and two smaller chromosomes, lying end to end. However, root tips of a normal *Populus tremula* from Källstorp gave a number of plates, in which the chromosome number was clearly 38 (Fig. 1). Of the gigas type less material was available but in several metaphase plates (cf. Fig. 2) the number was found to be ± 57. The average size of the chromosomes is the same in the diploid and triploid.

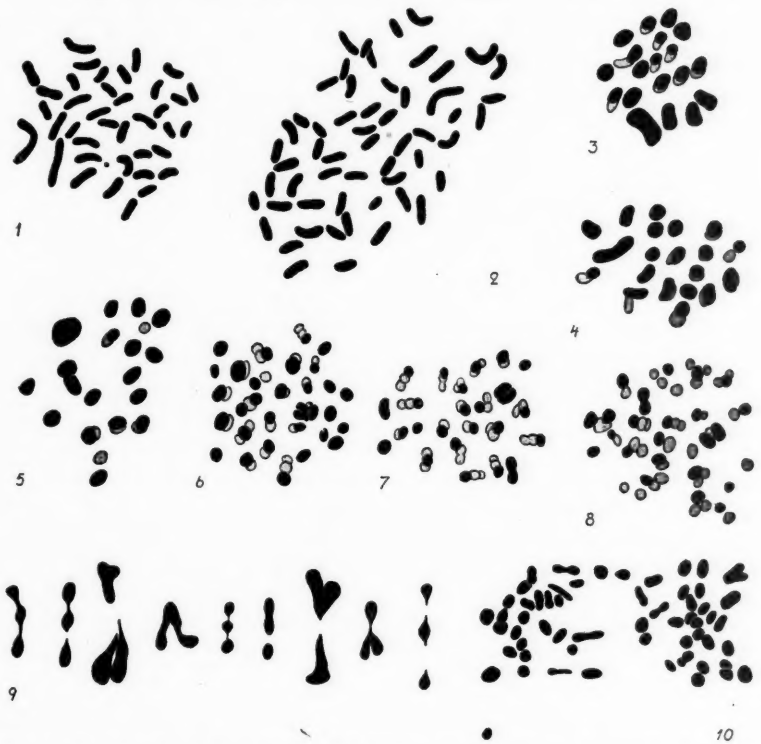
TABLE 1. *Length of stomata in diploid and triploid Populus tremula.*

	Length of stomata									n	M ± m
	6	7	8	9	10	11	12	13	14 units		
Diploid	3	21	18	25	16	6	1			90	$8{,}58 \pm 0{,}14$
Triploid.....			3	12	23	26	19	6	1	90	$10{,}76 \pm 0{,}13$

The somatic chromosome numbers were verified by preliminary studies of meiosis. Twigs of the gigas type as well as of the normal type from two different localities were put in water and placed in a moderately warm green house. After a week or a somewhat longer time the catkins had developed far enough to be used for meiotic studies. As *Populus tremula* is a dioecious species the triploid clone might be male, female or intersexual. Fortunately it proved to be purely male, the twigs producing typical male catkins. — The anthers were fixed in Carnoy or in chrome-acetic-formalin after prefixation in Carnoy. The right stage of fixation was ascertained by means of aceto-carmine preparations. For comparison anthers of normal *Populus tremula* were obtained and fixed in the same way. The study of meiosis gave the following results.

In normal *Populus tremula* meiosis was found to be regular, and 19 bivalents are generally present at first metaphase (Fig. 3). Sometimes, however, a few univalents were observed. In polar view these are difficult to distinguish from the bivalents, but the plates represented in Figs. 4—5 probably contain 18 bivalents + 2 univalents. As already described by BLACKBURN and HARRISON (1924) and observed from the somatic plates (Figs. 1—2), the idiogram of *Populus tremula* comprises chromosomes of different size classes. This is also strikingly evident from the first metaphase plates, in which one of the bivalents is much larger than the others (Figs. 3—5). Other meiotic stages were not studied in the diploid types but a few second metaphases in the material from Kågeröd had 19 chromosomes, as expected, and the tetrads were found to be quite regular. — Though rather limited these observations

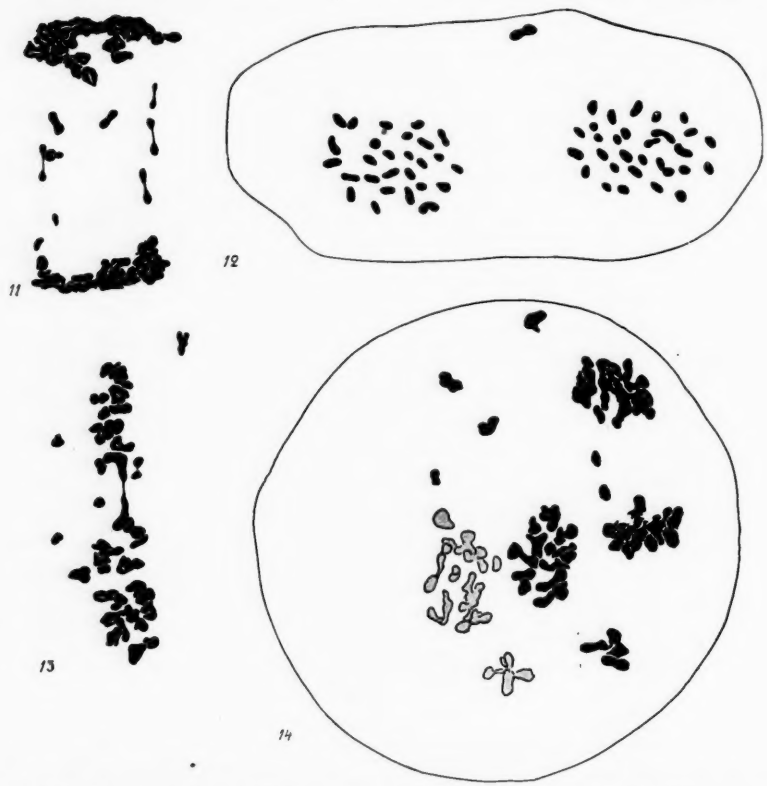
and the somatic counts are sufficient to show that ordinary specimens of *Populus tremula* in this province as well as in England have 2n = 38 and a regular meiosis, apart from the occasional occurrence of uni-



Figs. 1—2. Somatic plates. Fig. 1, diploid type from Källstorp (2n = 38); fig. 2, the triploid gigas type from Lillö (2n = ± 57). — Figs. 3—5, first metaphase plates in diploid types (figs. 3—4, material from Kågeröd; fig. 5, from Lillö); fig. 3, 19_{II}, figs. 4—5, probably $18_{II} + 2_{I}$. — Figs. 6—8, I—M (polar view) in the triploid gigas type; fig. 6, about 29 separate bodies, comprising 5 clear trivalents and 12 clear bivalents; fig. 7, 24 separate bodies, probably $13_{III} + 7_{II} + 4_{I}$; fig. 8 (commencing anaphase), 57 chromosomes may be distinguished, approximately corresponding to the formula $11_{III} + 7_{II} + 10_{I}$. — Fig. 9, types of trivalents in the gigas type from different I—M in side view. — Fig. 10, I—A in the gigas type, ± 57 chromosomes may be distinguished. — × 3600.

valents. To state it clearly, the male clone from Källstorp had 2n = 38 in root tips (Fig. 1), material from Kågeröd (a short distance north of Källstorp) showed 19_{II} or $18_{II} + 2_{I}$ at first metaphases and 19 chromo-

somes in a few second metaphase plates. Finally, a male tree of normal appearance, growing close by the triploid gigas clone at Lillö, also had the same chromosome number. Of this tree only a few first metaphases



Figs. 11—14. Meiosis in the triploid gigas type (continued). Fig. 11, first telophase with lagging chromosomes; fig. 12, II—M, both plates in the same plane, in the plate to the left 26—27 chromosomes, in the other plate 29—30, the eliminated body corresponds to one or possibly two chromosomes, minimum total number of chromosomes = 56, maximum = 59; fig. 13, fusion of II—M plates will lead to formation of dyads; fig. 14, II—A with 6 anaphase groups + several eliminated chromosomes. — × 3600.

were available, but one of them most probably represented $18_{II} + 2_{I}$ (Fig. 5).

The mode of meiosis in the triploid (Figs. 6—14) is quite different and characterized by great irregularity and the presence of trivalents at

first metaphase in addition to bivalents and univalents. First metaphases in side view could not be completely analysed, but a number of separate trivalents from different metaphase groups are represented in Fig. 9. These trivalents are composed by chromosomes of markedly different size. Two of them (Nos. 3 and 7 from the left) most probably correspond to the giant chromosome present in diploid *Populus tremula*. This chromosome is consequently represented twice in the diploid, three times in the triploid gigas type. Judging from Fig. 9, most of the trivalents are straight chains, Y shaped configurations also occur, and more rarely trivalents of the V type (No. 6 from the right) are formed.

The trivalents could also be distinguished fairly well in polar views (Figs. 6—8). In Fig. 6 there are about 29 separate bodies, comprising 5 clear trivalents and 12 bivalents. The remaining bodies are not visibly double but must consist of bivalents as well as univalents. The very large chromosome mentioned above and occurring three times in the triploid is probably represented by one bivalent and one univalent in this metaphase group. Fig. 7 represents another I—M, in which the number of trivalents is evidently rather high. The chromosomes in this cell are probably associated according to the formula $13_{III} + 7_{II} + 4_{I}$. If this interpretation is correct the total number of chromosomes would be 57. The number of trivalents may have been still higher somewhat earlier. Judging from their position, one bivalent + one univalent at 8 o'clock in the plate (Fig. 7) have earlier been the constituents of a trivalent. Consequently, as many as 42 (14×3) of the 57 chromosomes may be united to trivalents in the gigas type.

The best polar view of a I—M, or in this case a slightly later stage, is represented in Fig. 8. In this cell the total number of chromosomes is evidently 57 or very near this number. As the chromosomes are in a commencing anaphase their configurations cannot be determined quite accurately. However, there are approximately $11_{III} + 7_{II} + 10_{I}$. The high number of univalents is probably in part caused by the advanced stage. The large chromosome in this cell is probably represented by a trivalent.

A comparison between the I—M chromosomes in the diploids (Figs. 3—5) and the triploids (Figs. 6—8) seems to show that the chromosomes in the triploid gigas type are smaller than in the diploid types. This, however, is only apparent, different fixatives having been used. The chromosomes of the diploids are swollen on account of fixation in pure Carnoy. The fixation, giving the best results in the triploid, was a

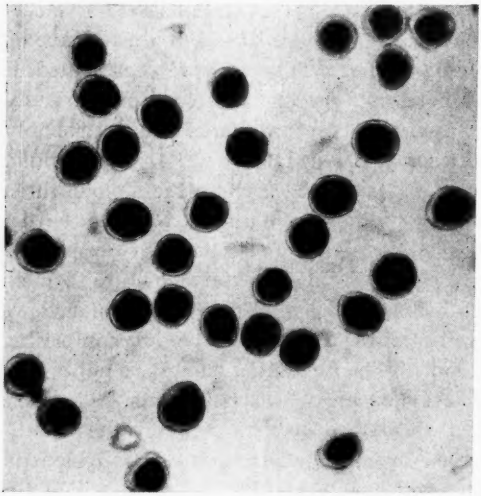


Fig. 15. Pollen grains of diploid *Populus tremula*.

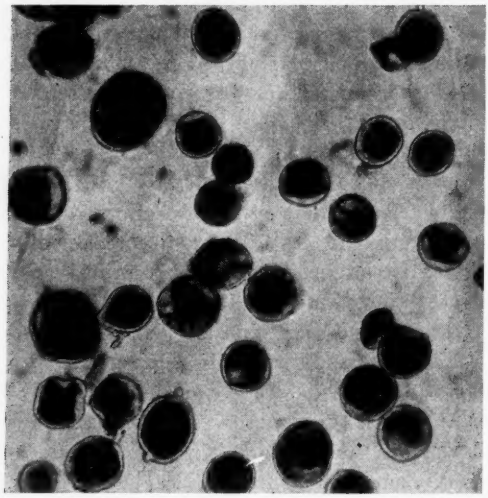


Fig. 16. Pollen grains of triploid *Populus tremula*.

chrome-acetic-formalin fixation with only a short preparatory treatment in Carnoy.

Approximately 57 chromosomes were again counted in the I—A group drawn in Fig. 10. It is uncertain, however, whether some of the lagging chromosomes in this group are half, whole or double. A certain amount of irregularity is evident in this anaphase. This is still more evident from the first telophase given in Fig. 11. The lagging univalents have here a strong tendency to divide, but it is uncertain whether this division will ever be completed.

One of the best opportunities for making an accurate determination of the chromosome number in the gigas type was offered by the pollen mother cell represented in Fig. 12. In this cell the two II—M plates were orientated in the same plane and both of them could be counted. Though the fixation in this cell is unusually good each plate contains one doubtful point. At these points it is uncertain whether there is one large chromosome with a marked median constriction or two small chromosomes.

It is quite sure, however, that the plate to the left contains 26 or 27 chromosomes, the other plate 29 or 30 chromosomes. The large eliminated body, lying at the side of the cell, may also correspond to one or possibly two chromosomes (members of a former trivalent). Consequently, the minimum total number of chromosomes must be 56 and the maximum number 59. The second anaphases are sometimes rather regular but sometimes rather abnormal. Fig. 14 represents such a cell in which there are six different anaphase groups and a number of eliminated chromosomes.

As a consequence of such irregular divisions the tetrads were often rather irregular and contained microcytes in different numbers. As is evident from Fig. 13, dyads may also be formed. The II—M plates are in the same plane and united by a chromosome pair (probably corresponding to the very large chromosome), the members of which have failed to disjoin. Fusion of the homotypic spindles in this way is a well-known phenomenon, which has been described in many hybrids.

The quality and appearance of the pollen (Fig. 16) is in accordance with the irregular meiosis in the triploid. A large proportion of the grains are visibly defective and the variation in size is very marked. Some grains are strikingly large. In normal, diploid *Populus tremula*, on the contrary, the pollen is quite good and uniform in size (Fig. 15). In order to study this difference in quality and size some countings and measurements were made.

The pollen grains observed were divided into 3 categories: perfectly good, dubious and obviously bad grains. Pollen samples from the gigas type and from the diploid *Populus tremula* from Kågeröd were compared with the following results:

	Number of			
	good,	dubious,	bad grains	n
Triploid:	190	126	117	433
Diploid:	563	41	53	657

According to these values the percentage of good, dubious and bad grains is 44, 29 and 27 in the triploid, the corresponding values in the diploid being 86, 6 and 8 respectively. The contrast is very striking (cf. Figs. 15—16) and strongly indicated an unbalanced chromosome number in the gigas type already before the triploid number of this type had been determined.

The relative size and variation of the pollen has also been calculated (Table 2). Only good or somewhat dubious grains were measured,

TABLE 2. *Pollen size in diploid and triploid Populus tremula.*

	Pollen diameter																	n	M
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	units		
Diploid	8	60	102	28	10													208	9,87
Triploid	7	13	41	61	84	68	37	26	9	20	28	9	2	—	1	2		408	13,04

the bad grains being shrunken and unsuitable for measurements. As might be expected, the pollen grains of the diploid are on an average smaller and less variable in size than those of the triploid. The series obtained for the triploid is obviously bimodal. This is probably due to the fact that a certain percentage of unreduced pollen grains is formed as indicated by the meiotic irregularities described above (cf. Fig. 13). The first maximum in the series, which approximately corresponds to the chromosome number 57/2, is situated at 12 units, the second maximum at 18. The volume of the unreduced grains is evidently at least twice as great as the average volume of the reduced grains. A low frequency of still larger pollen grains was also observed. A few such giant grains may be seen in Fig. 16 and the possible occurrence of a third maximum in the triploid series (Table 2) is indicated by the few grains having a diameter of 22—23 units. During the meiotic observations some giant pollen mother cells containing several nuclei were observed. Such cells may be responsible for the production of pollen grains with more than 57 chromosomes.

From the report given above it is evident that the giant aspen type from Lillö is autotriploid in contrast to normal *Populus tremula*, which is diploid. The somatic chromosome numbers are ± 57 and 38 respectively. Though it is highly probable that the chromosome number of the triploid is exactly 57, it has not yet been possible to determine the number with absolute accuracy. The number, however, cannot be lower than 56 and not higher than 59 (Fig. 12). Considering all the data, it seems safe to conclude that the 2n value of the gigas type is within the limits 56—58.

That the gigas type is auto- and not allotriploid is evident from the high frequency of trivalents at meiosis, at least 42 of the 57 chromosomes (74 per cent) being observed to occur as trivalents (Fig. 7). The autotriploid nature of the gigas type is further supported by the observation that one conspicuously large chromosome is present twice in the diploid and most probably three times in the triploid.

Just as in the case of many other autotriploids (cf. MÜNTZING, 1931, p. 3) the triploid aspen must have arisen from the union of one reduced and one unreduced gamete. Being a tree, the triploid thus arising has been able to persist through a long period of years, and thanks to spontaneous vegetative propagation it is now represented by a rather large clone. The instances of triploids arising in that way are very numerous. This has also happened in another tree, occurring in Sweden, viz. *Acer platanoides*. MEURMAN (1933) determined the chromosome number of 22 seedlings of that species and found that one of them was triploid with $2n = 39$, the others being diploid with $2n = 26$. No full-grown triploid specimens of *Acer platanoides* have been found so far.

As *Populus tremula* is a dioecious species, in which sex chromosomes seem to occur (BLACKBURN and HARRISON, 1924), the triploid clone, in analogy to *Drosophila* and *Rumex acetosa* (cf. ONO and SHIMOTOMAI, 1928; ONO, 1935), might be expected to be intersexual. As already mentioned, however, it seems to be purely male, judging from the male catkins obtained from twigs placed in a green house. Further discussion of this problem will be postponed, pending more thorough morphological and cytological investigations.

The striking morphological characters of the triploid *Populus tremula* are, no doubt, in the main caused by the increased chromosome number. As is well-known and as discussed in detail by the present writer (MÜNTZING, 1936) experimental and spontaneous autopolyploids are generally gigas types in comparison with their corresponding diploids. This is chiefly due to the increased cell size which is strongly correlated with the chromosome number. As shown above, the triploid *Populus tremula* had larger stomata and pollen grains than diploid aspen. This is probably true of the other cells as well. It should further be remembered that autopolyploids are not only morphologically altered but generally also have new physiological properties as compared to the diploids (cf. MÜNTZING, 1936, pp. 293—298). Whether this is true of the giant aspen remains to be investigated.

On account of its economical value it would be desirable to obtain progeny from the triploid gigas type and try to select still better types of *Populus tremula* among its descendants. For this work the possibility of vegetative reproduction is of prime importance. As the aspen is dioecious and the gigas clone male the only way to obtain progeny is from the combination normal diploid ♀ × triploid gigas ♂. Fortunately, the triploid does not seem to be entirely sterile. At least under green house conditions plenty of pollen is shed and a fairly high percentage,

about 44 per cent, is morphologically good. In analogy to other crosses between diploid and triploid types of other species it may be predicted that if this cross succeeds most of the progeny will have the diploid chromosome number 38 or somewhat higher numbers, but only those which have exactly the diploid number will have normal viability. Even these plants, however, will most probably be inferior in vigour compared to the triploid gigas type.

Fortunately, there is another possibility of obtaining vigorous progeny. The curve obtained from measurements of the pollen in the triploid was found to be bimodal, this being due to the observed formation of unreduced pollen grains. The chance that these pollen grains will be functional is rather high, judging from the behaviour of many other triploid hybrids. Therefore, in addition to individuals having approximately the diploid number 38 the cross diploid $\times$ triploid *Populus tremula* may also give tetraploid individuals with $\pm$ 76 chromosomes.

To take a comparable instance, the tall and vigorous banana variety *Gros Michel* is a triploid commercial variety of high economical importance (CHEESMAN, 1932). The chromosome number of this variety is 33, the basic number being 11. By continued breeding, viz. from the cross *Gros Michel* $\times$ a diploid variety as the male parent, new tetraploid products with $2n = 44$ were obtained in the progeny. It was found that in the triploid mother clone gametes with the unreduced (and even twice the unreduced) chromosome number were formed. The new tetraploid products arising in this way seem to be economically valuable.

Thus, although the production of tetraploid descendants from the triploid giant clone of *Populus tremula* is theoretically possible it is uncertain whether such products will be superior to the triploid type. It is now well-known (cf. MÜNTZING, 1936, p. 286) that there is an optimum for the increase in chromosome number and that this optimum has rather different values in different species. At any rate it would, however, be extremely interesting to undertake further breeding work in combination with cytological studies with this material.

Finally, it should be emphasized that the finding of the giant *Populus tremula*, which is the result of Nature's own experiments, strikingly demonstrates the great possibilities of experimental breeding work with forest trees and fruit trees. It also demonstrates the importance of cytological control during such work and stresses the possibility of producing new improved varieties with an increased number of chromosomes.

SUMMARY.

1) A giant form of *Populus tremula*, detected by Professor H. NILSSON-EHLE and cytologically examined by the present writer, was found to be triploid, having $2n = \pm 57$. Ordinary *Populus tremula* from three different localities in South Sweden had $2n = 38$. The giant characteristics of the triploid must be due to the increased chromosome number.

2) A preliminary study of meiosis showed that the gigas form is autotriploid, trivalents in addition to bivalents and univalents being frequent at I—M in the p.m.c. The triploid, which is male, must have arisen from the union of one reduced and one unreduced gamete.

3) The formation of unreduced gametes in the triploid was indicated by meiotic observations and is reflected by a bimodal curve with regard to pollen size. This opens a possibility of obtaining tetraploids from the cross diploid $\times$ triploid by future breeding work.

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